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Parasitology and Pathology of Marine Organisms of the World Ocean

William J. Hargis, Jr. (Editor)

March 1985

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William J. Hargis, Jr. (Editor)

March 1985

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FOREWORD

The Symposium in which the communications, as they were called during the meeting, comprising this volume were presented was held at the Zoological Institute of the Academy of Sciences of the U.S.S.R. in Leningrad during 13 to 16 October 1981. Conducted as part of the cooperative program of the U.S.A.-U.S.S.R. Working Group on Biological Productivity and Biochemistry of the World Ocean, the Leningrad meeting was sponsored by the Academy of Sciences of the U.S.S.R. (the Zoological Institute) and the Ministry of Fisheries of the U.S.S.R. (The Scientific Council on Fish Diseases of the Ichthyological Commission). It was an extremely interesting and successful Symposium, offering all participants the opportunity to describe the results of their studies and reviews during the course of the formal presentations and direct interchange between scientists during breaks in the program and the organized and casual social activities. The facilities provided by the Zoological Institute were quite adequate and the assistance offered by its Director, O. A. Scarlato and his staff in organization, logistics, and translation was excellent. Several of our Soviet colleagues presided over the proceedings, as did I. All were businesslike and efficient, yet graceful and accommodating. To O. N. Bauer fell the brunt of programmatic detail and follow-up. He bore his burdens well and, with Director Scarlato and his staff, including A. V. Gussev and others of the professional and technical staffs of the Zoological Institute, helped make our stay pleasant and the Symposium productive. These organizations and individuals deserve much credit and praise as well as the thanks of their American and British colleagues.

William J. Hargis, Jr.

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[1]Organized into groupings according to types or classes of papers into which several communications can be placed, albeit somewhat arbitrarily.

[2]As employed in these communications, the words trematode or trematodes means Digenea or digeneids, respectively. Most Russian parasitologists accord Class status to Trematoda or Digenea as well as to Monogenea or Monogenoidea.

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Parasitology and Pathology of Marine Organisms of the World Ocean

Proceedings of the U.S.A.-U.S.S.R. Symposium conducted within the program "Biological Productivity and Biochemistry of the World Ocean" held at the Zoological Institute of the Academy of Sciences of the U.S.S.R., Leningrad, October 13-16, 1981[1]

WILLIAM J. HARGIS, JR. (Editor)[2]

INTRODUCTION

Background of the Symposium

In 1973 the President of the United States of America and the Premier of the Union of Soviet Socialist Republics signed an agreement establishing the common interest of the two countries in the phenomena and problems of the World Ocean and calling for cooperative studies. The resulting joint activities, which involved programs in a number of scientific areas, were placed in the hands of a combined U.S.A.-U.S.S.R. Committee to provide general guidance and oversight and maintain high-level communications. The different disciplinary or operational segments of the several programs were assigned to the control of several joint U.S.A.-U.S.S.R. subcommittees called Joint Working Groups. That portion of the programmatic activity dealing with nonfisheries biological phenomena and processes was placed under the Joint Working Group on Biological Productivity and Biochemistry of the World Ocean. Early on, the Chairmen and members of the Joint Working Groups met to arrange mutually suitable activities, which included exchanges of scientists, jointly sponsored symposia, conferences, or workshops as well as cooperative publications, expeditions, and other projects of mutual interest. These programs and projects were solemnized in formal working agreements or protocols which included lists of the activities planned for the period in question. The overall program, due to expire in 1981, has been extended for three more years, until 1984.

The last formal protocol of the Working Group on Biological Productivity and Biochemistry, developed and signed in Tallin (Estonia) U.S.S.R. in 1979, called for two companion symposia on parasites and pathogens of marine organisms of the World Ocean. One was to be held in each nation to affort maximum opportunity for participation by scientists of each and for significant interchange of information.

For various reasons the first symposium did not take place until fall of 1981 in Leningrad, U.S.S.R. We hope that the second or reciprocal meeting in the United States will be convened within a year or two.

The 1981 meeting, hosted by the Zoological Institute of the Academy of Sciences of the U.S.S.R., involved over 45 Soviet scientists along with 4 from the United States and 1 from Great Britain. Pretranslated or instantaneously translated reports were presented by most participants. It was agreed that acceptable papers would be published in both languages in the respective countries.

The Symposium was extremely productive. The program involved about 50 oral communications or papers on a wide variety of subjects related to the general topic—marine parasitology and pathology. In accordance with the publication plan, the Soviets have already or are now presenting the reports in their national language through the normal publication channels open to them. Many were published in a single appropriately titled volume printed and released in Leningrad in 1981 (Bauer et al. 1981). Communications not included in that volume are being published in appropriate journals in the Soviet Union.

The volume at hand, designed to provide English-reading audiences with the results of the Symposium, includes all of the communications or papers whose authors have agreed to their publication and made them available. It is hoped that it will serve to indicate the wide variety of topics discussed and demonstrate the extent and productivity of Soviet workers in this important field of biological oceanography or marine ecology. Only five non-Russian scientists were able to participate, for various reasons. Their contributions, though noteworthy and valuable, were overshadowed by those of the numerous Soviet speakers, as would be expected.[3]

But the Soviet contributions were impressive in more than number or bulk. They reflected the emphasis that Soviet marine science places upon parasites, pathogens, and diseases of sea and marine organisms. They also indicated the magnitude of the Soviet biological and fishery research efforts in the World Ocean. Personnel of their numerous fishery reconnaissance and fishery research vessels, biological research ships, and the many elements of their world-ranging fishing fleet have assisted in this work by making parasitological collections themselves or by providing collecting and research platforms for many of the specialists involved.

[1]Contribution No. 1170 from the Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062.

[2]Professor of Marine Science, The School of Marine Science and The Virginia Institute of Marine Science, The College of William and Mary in Virginia; and U.S. Co-Chairman of the U.S.A.-U.S.S.R. Working Group on Biological Productivity and Biochemistry of the World Ocean.

[3]Several Soviet participants and our Welsh colleague (Jack Llewellyn) chose not to have their communications presented here, otherwise the number of papers presented in this volume would be greater. Also some who apparently did want their papers included did not or could not answer my plea for translations, abstracts, and references. In such cases the papers are presented as they were available, with appropriate editing or as we were able to translate and fill them out ourselves.

Without disparaging the significant and valuable efforts of other countries, including our own, the magnitude of Soviet research activity in the parasites, pathogens, and diseases of marine organisms, especially those of direct or indirect economic importance, is impressive. Russian scientists have made major contributions in fundamental and applied parasitology and pathology of the World Ocean as well as of their own coastal waters and interior seas. Thousands of individual hosts were involved in many of their faunistic and zoogeographic studies—some projects used many thousands apiece. Hundreds of host species have been studied and many are reported in this volume. Our Russian colleagues deserve much credit for their great interest, activity, and productivity in this vital field.

In preparing the papers for this volume every effort has been made to remain faithful to the first translations provided or to the originals where translations have been made locally. In many instances extensive editing was required to make them readily intelligible to English readers. In these presentations the editor's interpretations of the meaning of obscure or unusual words or phrases (to American readers) has been included in brackets after the words or phrases in question in order that the author's words could be retained. I regret and apologize to the original authors or translators, where their versions are significantly different from those presented herein (and I hope there are few), for any divergences from original meaning which may have been introduced in the extensive editing process.

It is hoped that this volume will convey to the reader the scope and detail of the communications contributed by Soviet colleagues as well as our own and will prove a useful addition to the world literature of parasitology and pathology.

Organization of the Volume

Developing a suitable organization for this volume was difficult. The papers presented during the symposium were varied in topic, scope or range, emphasis, and extent. Some were historical, dealing with past and current activities in research on parasites and pathogens. Some were reviews. Some presented findings in general fashion. Others were quite specific in treating results of recent research. A few dealt with the practical aspects of fishery parasitology and disease studies such as the effects on perishability (shelf-life), attractiveness, and marketability of fishery products and even their possible effects on the health of humans. Several presented discussions of the effects of diseases and parasites on fish and invertebrates under culture and techniques of dealing with them. A larger number dealt with parasites as bioindicators, useful in studies of paleogeography, zoogeography, and phylogeny of their hosts. Zoogeographical topics are significant in a number of them. A few treated quite different aspects such as the influence of parasites on the physiology of their hosts, and one dealt with the possible use of pigmented macrophage accumulations as indicators of fish health or of stress from anthropogenic pollution. Certain presentations focused on single major taxonomic groups (mostly classes) of parasites and pathogens, while others dealt with a number of different classes or even phyla in a single paper. The largest number of presentations (communications) treated fish as hosts, with those dealing with mollusk and crustacean hosts ranking as distant seconds and thirds, respectively. One paper, which had to be translated from the Russian to be included here, dealt with parasites of marine mammals.

With such a diversity of presentations as were made during the Symposium, any selection of organizational arrangement for this publication could only be somewhat arbitrary. As shown in the Contents, general or historical papers are presented first (Items under II); those dealing with parasites and pathogens of fish are second (Items under III); and those treating invertebrate hosts are third (Items under IV). One of the papers (Infectious Diseases of Fish Involved in Marine Aquaculture in the Soviet Far East, by Potievski et al.) treated both fish and mollusks now under culture in northeastern Russia and is interposed as a "bridge" between those offerings dealing with fish hosts on the one hand and invertebrate hosts on the other. The single paper on marine mammals is included under V.

There are two major categories—Parasites and Pathogens of Fish, and Parasites and Pathogens of Invertebrates. Within the first category, which is the larger, the organization into subcategories is as follows: 1) Mixed major parasitic taxa, 2) individual major taxa (i.e., protozoans, digeneids, monogeneids, cestodes, acanthocephalans, nematodes, and crustaceans, which may, along with viruses and bacteria, all be included in the "mixed major parasitic taxa" subcategory mentioned above), and 3) miscellaneous. The miscellaneous parasite topic or subcategory includes the pigmented macrophage accumulations offering of Wolke et al. as well as the Russian offering dealing with pathogens of salmon and mollusks in the "aquatoria" of the Soviet far east (Potievski et al., cited above).

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A large number of individuals are due acknowledgments and thanks for their assistance in the preparation of this volume. I must especially mention O. N. Bauer of the Zoological Institute of the Academy of Sciences of the U.S.S.R. who contacted and stimulated our Russian colleagues to provide their communications or papers. Those who responded to his urgings should be thanked also. Since their names are included with their offerings, they will not be listed here.

A number of my associates here at the Virginia Institute of Marine Science of the College of William and Mary must be mentioned with appreciation. Included are: Alice Lee Tillage, Shirley O. Sterling, and Regina A. Marsh for assistance with typing the several early drafts of the original manuscript and Annette C. Stubbs, Dorothy M. E. Smith, and Ruth A. Edwards of the VIMS Word Processing Unit for later drafts.

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Robert L. Edwards, immediate past Director of the Northeast Fisheries Center and my able associate in the workings of the U.S. half of the Joint Working Group on Biological Productivity and Biochemistry of the World Ocean, encouraged the entire program and provided support from the Center. Helen F. Mustafa has assisted in her service as NMFS Project Manager. O. A. Scarlato, Director of the Zoological Institute in Leningrad, provided the facilities and staff assistance which made the Symposium possible. To all of these individuals and to Carl J. Sindermann of the National Marine Fisheries Service, into whose competent editorial hands the manuscript was delivered, my appreciation and thanks.

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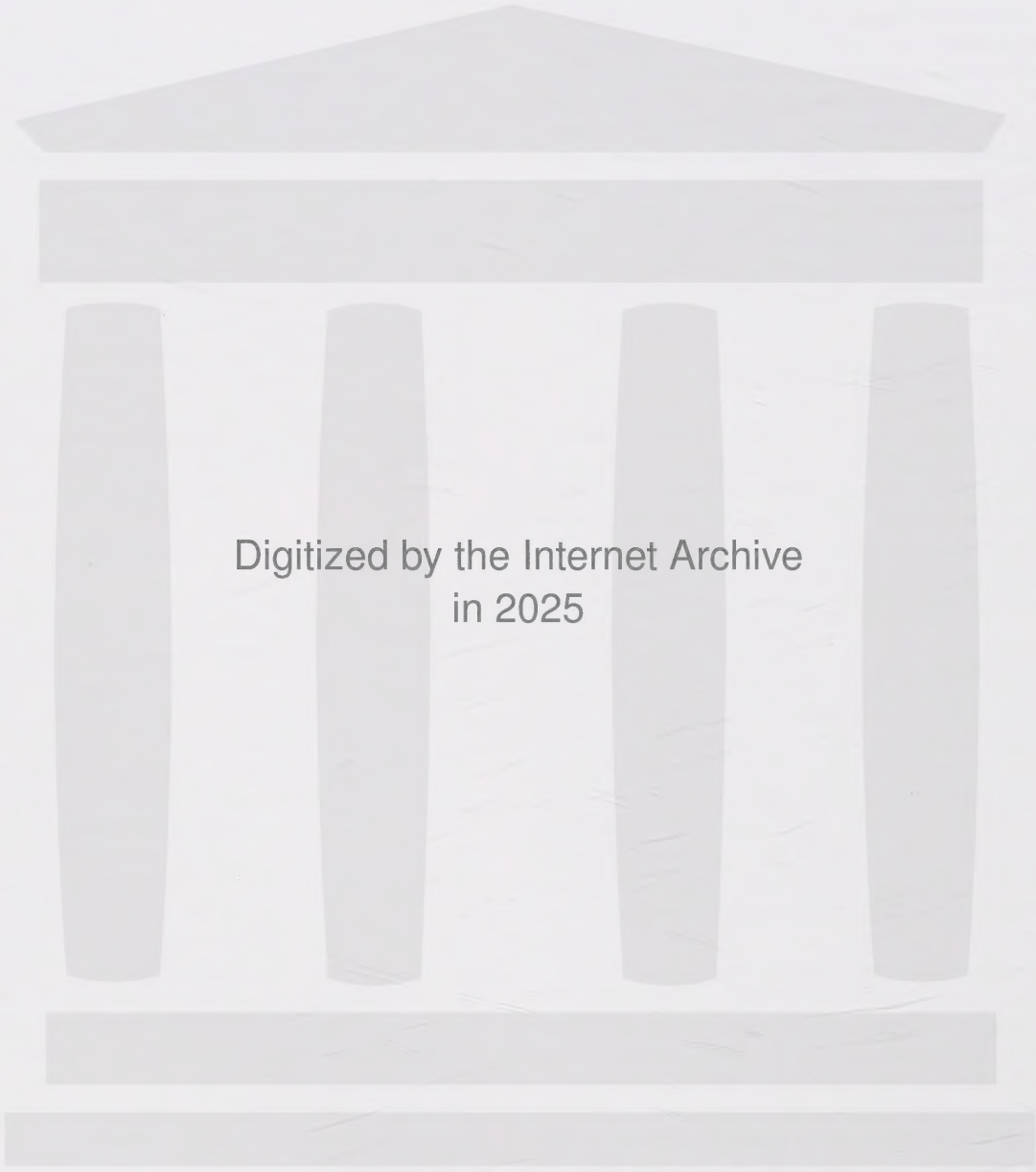

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Present State and Perspectives of Soviet Investigations on Marine Parasitology

O. N. BAUER[1] and Yu. I. POLIANSKI[2]

ABSTRACT

Soviet investigations in marine parasitology are reviewed. During the first half of this century the parasites of fishes living in inland rivers, lakes, and ponds, and, to a lesser extent, those of fishes of the inland (Aral and Caspian Seas) and adjacent seas were studied. At the end of the 1950's, long-term studies of marine organisms in different parts of the World Ocean were undertaken. Less work has been done on parasites and diseases of cultured sea organisms because mariculture is as yet poorly developed in the U.S.S.R.

Investigations of parasites and diseases of sea fishes in the Soviet Union were begun in the early 1930's. This happened after the organization of the first department on fish diseases by our prominent zoologist and parasitologist, Professor Valentin Dogiel. The first expeditions of this department were to the Aral Sea in 1930 and to the Caspian Sea in 1931-32. The materials gathered were not only faunistic. Data on the biology of the parasite fauna and on the influence of the environment on the fish contributed to the development of ecological parasitology. The influence of salinity on parasitic infection of fishes was discussed thoroughly in the publications by Dogiel and Bychovski (1934, 1938) based upon these data. It has been shown that the parasite fauna of fishes of the Aral Sea is truly freshwater in nature. But in the Caspian Sea brackish and sea (marine) elements have been found. The use of parasites as indicators of local fish stocks was discussed for the first time.

During the second half of the 1930's, parasitological data were gathered from Black Sea fishes. The paper of Osmanov (1940) dealing with these data is especially noteworthy.

Investigations of fish parasites from the Pacific region had been undertaken earlier by Layman (1930). In 1937 an expedition of Leningrad University, headed by V. Dogiel, began investigations of the parasites of fishes and invertebrates of the Sea of Japan. Yu. I. Polianski, M. M. Isakova-Keo, and A. V. Gussev participated. Materials dealing with parasitic Protozoa of fishes (Dogiel 1948), Mollusca and Echinodermata (Polianski 1951a, b), and parasitic Copepoda (Gussev 1951) from this expedition were published in postwar years. Interesting data on the parasite fauna of *Leuciscus brandti*, a migratory cyprinid, were also published by Isakova-Keo in 1952.

In postwar years investigations of marine parasites increased. A long-term survey of parasites of fishes and shellfishes of the Barents Sea was accomplished by Polianski (1955) and his pupils, Uspenskaya (1960) and Chubrik (1966). The fish parasites of the White Sea were thoroughly investigated by Schulman and Schulman-Albova (1953). Helminths of fishes of Pacific seas [bights, bays or basins—coastal waters] were studied by Zhukov (1960), Strelkov (1960), and Oshmarin et al. (1960). A summary of all these materials was made by V. A. Dogiel in 1954. Many papers on Monogenea of Pacific fishes were published by B. E. Bychovski.

As can be seen, until the 1950's and 1960's, the chief work in marine parasitology had been done in the continental and adjacent seas of the Soviet Union.

At the end of the 1950's our country began a long-term program to increase catches of fish and other sea products in the open parts of the World Ocean. These catches increased up to 20 million tons in 1975. At the beginning of the program it was discovered that fish stocks of several species in some parts of the World Ocean are heavily infected by parasites and could not be used for consumption. Since then the problems of marine parasitology have been recognized to be of economic importance, and the need for special departments has been emphasized. The Department of Marine Parasitology of the Institute of Biology of Southern Seas in Sevastopol headed by V. M. Nikolaeva became the first such department. It began its investigations in 1958. Later, similar departments were organized in the Research Institute of the Ministry of Fisheries. In 1966 [two were established], one in the Pacific Institute (TINRO)—headed by Yu. V. Kurochkin—and the other in the Atlantic Institute (AtlantNIRO)—headed by A. V. Gaevskaya, and others. At the beginning of this program, work on helminths dominated. Since then attention has been given to other groups of parasites—Protozoa (especially Myxosporidia) and Crustacea (both Copepoda and Isopoda). During the last 20 yr an enormous amount of materal has been gathered. Summaries of much of this work will be presented in the contributions to this Symposium.

We now have trained and experienced scientists with expertise in different groups of parasites who can solve problems of theoretical and economic importance. Some examples of the last: Of great economical value are the investigations of the TINRO parasitologists on how to trim carcasses of teragra, *Theragra chalcogramma*, that are heavily infected by tetrarhynchids. Scientists of the Zoological Institute and AtlantNIRO have worked out recommendations connected with pelagic fishes infected by Myxosporidia—Multivalvulea of the genus *Kudoa*. This parasite causes muscle lysis in stored fish.

Less research has been done on parasites of shellfishes but during the last several years it has increased. Several papers of this Symposium will be devoted to this problem. An example is the research in the Barents and White Seas on ecology, histology, and physiology of some trematodes heavily infecting fish and seabirds.

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The parthenogenetic stages of these species infecting mollusks have been thoroughly studied using cytochemical and electron-microscopical (ultramicroscopical) methods. Such methods help us to understand the host-parasite relations of the system. The results of this research, done by A. A. Dobrovolski, K. V. Galaktinov, and I. A. Tichomirov, have shown that recent ecological parasitology, marine parasitology included, must be done not only on the organismal but also on cellular and molecular levels.

Until now little has been done in our country in the culture of fish and shellfish in coastal waters. But during recent years more attention has been given to this area. Experience of other countries, especially the United States, Japan, and England, has shown that such culture is often accompanied by mass diseases, the causative pathogens of which are not only parasites of animal nature, especially those lacking intermediate hosts (i.e., Protozoa, Monogenea, and parasitic crustaceans), but of others in different systematic positions such as bacteria, viruses, and fungi. During the last decade a large number of such diseases of marine and anadromous fish have been described. Many are of great economic importance in mariculture.

In our country the earliest experience in such diseases was obtained when culture of salmonids was begun in the coastal waters of the Baltic Sea. *Vibrio anguillarum* was the first pathogen of economic importance studied. BaltNIRKH and its branch in Tallin [Estonia] have studied this disease and employed methods of control, including immunoprophylaxy. Vaccines from the German Democratic Republic and the United States have been examined with good results. However, an increase of such research in mariculture is greatly needed.

It is also noteworthy that the experience of Soviet fish parasitologists in seafish culture has shown that even widely distributed parasites, which are described as harmless, can act as pathogens. Scientists of the Zoological Institute have described mortalities of young White Sea herring infected by only a few specimens of trematodes such as members of the well-known *Lecithaster* and *Brachyphallus* genera. Fish parasitologists from other countries have also described such cases. The same will be said when we discuss the culture of shellfish.

By the end of the 1960's, the urgency of coordinating research in parasitology and pathology of sea organisms was clearly recognized. In 1970, the first All Union Symposium on Parasitology sponsored by the Council on Fish Diseases of the Ichthyological Commission was held in Sevastopol with great success. The second took place in Kaliningrad in 1976. Now we are gathered for the third time, but this time with our colleagues from the United States and one from Great Britain. During the first two Symposia little attention was paid to pathology of marine organisms, especially cultured ones. We hope that this problem will be thoroughly discussed at this Symposium.

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Recent Studies on Marine Fish Parasites and Diseases

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ABSTRACT

Progress in research on marine fish diseases and parasites in the United States can be discussed in three categories: Diseases and parasites in natural populations, disease in degraded habitats, and disease in marine aquaculture. Principal interest is in the effects of diseases on wild or cultured populations of economic importance, but there are subsidiary interests in diseases and parasites as indicators of environmental changes, in public health aspects of fish diseases and parasites, and in effects of parasites on market quality of fish products.

Studies of natural populations of fish have concentrated on pathogens and parasites which occur at epizootic levels. Important here are viral diseases, particularly viral erythrocytic necrosis, some bacterial diseases, such as that caused by *Pasteurella piscicida*, and a systemic fungus disease caused by *Ichthyophonus hoferi*. Attempts to quantify the effects of disease on fish abundance have increased, and there is growing acceptance of the conclusion that disease-related mortality is a significant environmental factor in the sea.

Recent emphasis has been placed on diseases which may be associated with estuarine/coastal pollution in the vicinity of human population centers. Several diseases and disease signs—notably integumental lesions such as ulcers, fin erosion, papillomas, and lymphocystis—have been associated (some only circumstantially) with environmental degradation. Chromosomal anomalies and developmental abnormalities (skeletal malformations) have been studied also, from the viewpoint of increased prevalences in polluted zones. An important role for facultative microorganisms—particularly bacteria of the *Vibrio*, *Pseudomonas*, *Aeromonas* group—has emerged. Evidence is accumulating for localized effects of pollutants on fish populations, and for the utility of certain disease signs as indicators of environmental stress.

The slow but continuous development of marine aquaculture in the United States has been accompanied by increasing attention to diseases and disease control. Sea cage rearing of Pacific salmon (genus *Oncorhynchus*) on both coasts has been possible only by control of vibriosis (principally *Vibrio anguillarum*). Effective polyvalent vaccines now limit the problem, but other diseases, such as bacterial kidney disease (BKD) and furunculosis (caused by *Aeromonas salmonicida*) persist. Additionally, certain salmonid virus diseases seem capable of transmission and of causing mortality of salmon in seawater.

Parasites which reduce market quality of marine fish include the histozoic myxosporidan Protozoa and larval helminths, particularly larval nematodes. Few of these are of public health concern, but many result in rejection of infected fish as food.

With the impetus provided by declining marine fish stocks, increasing coastal pollution, and developing aquaculture, fish disease research has expanded in recent decades. There is still a need for quantification of disease effects on population abundance.

INTRODUCTION

Many parasitological and pathological problems concerning marine fish are being addressed by scientists in a number of countries. Interest is focused logically on those which affect survival, either in natural or cultivated populations. Of the many topics which might be considered, I have selected the following four for discussion in this paper: 1) Vibriosis, 2) the emerging role of viruses in marine fish—especially IPN-like viruses, 3) blood Protozoa, and 4) fungus (*Ichthyophonus*) epizootics.

In discussing these categories, I will try to emphasize results obtained since 1970, recognizing that a number of the disease entities have been known and examined well before that date.

After this consideration of examples of progress in disease research in natural and cultivated fish populations, I would then like to consider pollution-associated diseases, and our present understanding of the relationship of estuarine/coastal pollution and fish diseases.

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VIBRIOSIS OF FISH

Vibriosis of marine fish has had a long history of attention by fish pathologists—beginning over half a century ago with "red disease" of eels caused by *Vibrio anguillarum* (Bergman 1909). Vibriosis has occurred at epizootic levels in wild populations as well as cultivated ones. Juvenile saithe, *Gadus virens*, have experienced repeated mortalities on the Norwegian coast due to *V. anguillarum* outbreaks, the most recent being 1967 and 1974 (Anonymous 1975). *Vibrio anguillarum* has also been identified as a pathogen of winter flounder, *Pseudopleuronectes americanus*, from the western North Atlantic (Levin et al. 1972).

With the continued development of marine aquaculture, the genus *Vibrio* has emerged as probably the most important pathogen group for fish and invertebrates (Sindermann 1977). *Vibrio* infections and *Vibrio*-caused mortalities have been reported for virtually every species which has been cultivated extensively in saltwater. Vibriosis has been characterized as a haemorrhagic septicemia, with lesions attributable to both exotoxin and endotoxin (Bullock and Conroy 1971; Umbreit and Ordal 1972; Harbell et al. 1979).

Probably nowhere have *Vibrio* infections been of greater consequence than in saltwater culture of salmonids. At times it seemed as if the continued existence of seawater cultivation of salmon

depended on successful solution of the vibriosis problem, and some aspects of the problem still exist today, even though remarkable advances have been made in disease control, particularly through immunization.

Sea pen culture of Pacific salmon of several species, but particularly of coho salmon, *Oncorhynchus kisutch*, began on the west coast of the United States in the early 1970's, and mortalities due to vibriosis were noted almost immediately (Harrell et al. 1975). Initial approaches to control emphasized antibiotic treatment, but oral and other types of immunization developed rapidly. Immunization by injection of juveniles with killed pathogens was effective but labor-intensive. This method has now been replaced by hyperosmotic spray and bath immunization, augmented when necessary by antibiotic treatment or use of furanace (where permitted) (Egidius and Andersen 1979). Oral immunization has also been demonstrated to be effective (Fryer et al. 1978). Polyvalent bacterins have been produced, and vibriosis, while still a problem, is now considered a controllable factor in salmon cultivation in the Pacific Northwest and in European waters. Vaccination is now part of the standard protocol for cultivation of Pacific salmon in sea cages in the northwestern United States.

Experience with vibriosis in cage culture of Atlantic salmon, *Salmo salar*, in the northeastern United States and in northern Europe has profited from advances made in the Pacific. The disease, for example, has been a threat to Norwegian cage culture, particularly in coastal areas where vibriosis epizootics have also occurred in wild populations of saithe.

An emerging phenomenon, both in North America and in Europe, is the appearance of new strains or serotypes of *V. anguillarum*, which must be incorporated into the immunization protocol (Sawyer and Towle 1976; Egidius and Andersen 1978). Bacterins of west coast origin have been augmented with fractions reactive with additional strains of Atlantic vibrios to control disease in U.S. east coast stocks. The probability of a large number of serotypes complicates bacterin production, and requires constant vigilance to detect new forms of the disease. Some cross-protection is provided by various vaccines, but not enough and not consistently.

Another emerging phenomenon is the appearance of some of the well-known salmonid diseases, such as furunculosis (caused by *Aeromonas salmonicida*), bacterial kidney disease (caused by *Renibacterium salmoninarum*), and Viral Hemorrhagic Septicemia (VHS)—which have been and continue to be serious hatchery problems—and causes of mortality in seawater as well (Frantsi et al. 1977; Castric and deKinkelin 1980; Paterson et al. 1981). These diseases may be carried in a latent state from fresh to saltwater, but furunculosis and VHS have been transmitted from fish to fish in seawater (Scott 1968; Novotny 1975; Castric and deKinkelin 1980). Novotny, for example, cited instances of mortalities in sea cages of chinook salmon, *Oncorhynchus tshawytscha*, of up to 80% in 5 mo, caused by simultaneous epizootics of furunculosis and vibriosis. The furunculosis organism in this study proved to be salt-tolerant, as well as sulfa- and oxytetracycline-resistant.

Other halophilic *Vibrio* species (*V. parahemolyticus*, *V. alginolyticus*, and *V. cholerae*) have also been involved, along with *V. anguillarum*, in diseases of cultivated shrimps, crabs, and mollusks in several countries (DiSalvo et al. 1978; Liebovitz 1978; Brown and Losee 1978). Vibriosis affects larval and juvenile stages in particular. Additionally, vibriosis was also responsible for high mortalities in juvenile turbot (*Scophthalmus maximus*) being farmed in the United Kingdom (Horne et al. 1977).

VIRUSES IN MARINE FISH

IPN-Like Viruses

Knowledge of viral diseases of marine fish has increased remarkably in the past decade. Much recent attention has been given to the so-called IPN viruses. A disease of salmonids known as Infectious Pancreatic Necrosis (IPN) was first described by McGonigle (1941) and its viral nature demonstrated by Wolf et al. (1960). Resembling a reovirus, the pathogen has since been described from a wide range of vertebrate and invertebrate hosts (including several species of mollusks) (Hill 1976; Underwood et al. 1977). Probably the most interesting recent finding in the United States is that a highly lethal and common disease of Atlantic menhaden, *Brevoortia tyrannus*, long known as "spinning disease," has been associated with infection of the central nervous system by an IPN-like virus (Newman 1980; Stephens, Hetrick, and Newman 1980; Stephens, Newman, Zachary, and Hetrick 1980).

The reports represent a satisfying conclusion to decades of uncertainty about the cause of annual mortalities of menhaden which have occurred at various locations on the U.S. east coast—and for which records of mass deaths extend back to the 18th century. The disease was transmitted by intraperitoneal injection; typical spinning signs were produced, and the virus was reisolated from experimental fish. The virus was antigenically similar to IPN. Subsequent exposures of menhaden and American shad, *Alosa sapidissima*, to water seeded with virus also produced infections. It is relevant that some gross signs of IPN infection are similar in menhaden and salmonids. The spinning behavior, exophthalmia, and heightened pigmentation are similar, but menhaden do not usually exhibit visceral hemorrhages.

Additionally, severe outbreaks of IPN-like virus have been reported in eels (*Anguilla japonica* and *A. anguilla*) from Japan (Sano 1976; Pilcher and Fryer 1980). The virus, antigenically related to IPN, and called EVE, has produced extensive annual mortalities in eel culture ponds. It has been transmitted directly and by inoculation in juvenile eels, producing mortalities of 55 to 60% of experimental fish. The virus was reisolated from moribund fish, and seems distinct from other viruses isolated from the blood of European eels with stomatopapilloma (cauliflower disease).

From these and other studies, it seems that the former narrow concept of IPN virus of salmonids must be broadened to include an entire array of IPN-like viruses from fish and invertebrates, and from freshwater, anadromous, catadromous, and marine fishes.

Viral Erythrocytic Necrosis

Among the blood parasites of fishes, much attention has been paid during the past decade to a disease known as "Piscine Erythrocytic Necrosis" (PEN). Viral etiology has been indicated in some studies, so the disease has been redescribed as "Viral Erythrocytic Necrosis" (VEN). Cod, *Gadus morhua*, have been found to be infected on both sides of the Atlantic (Laird and Bullock 1969; Reno and Nicholson 1980; Smail and Egglestone 1980). Other Atlantic species of commercial importance—herring (*Clupea harengus*), alewife, *Alosa pseudoharengus*, American eel, *Anguilla rostrata*, and rainbow smelt, *Osmerus mordax*—have been found to be infected (Doyle 1970; Sherburne 1973, 1977). Additionally, the disease has been recognized in Pacific salmon. Bell and Margolis (1976) reported a VEN-like agent associated

with an epizootic of cultured pink salmon, *Oncorhynchus gorbuscha*, in sea pens at Nanaimo, B.C., transmissible by injection to chum salmon, *O. keta*, and to other pink salmon. Subsequently the disease was found in several other species of salmonids (Evelyn and Traxler 1978) and in Pacific herring, *Clupea harengus pallasi*, in prevalences up to 59% (MacMillan and Mulcahy 1979). Heavily infected fish had surface hemorrhages.

The usual VEN disease signs—intracytoplasmic inclusions and nuclear changes, often with accompanying anemia—may occur in high prevalences. For example, up to 50% of the blood cells of cod were found to be infected in one study (Smail and Egglestone 1980). VEN has not been definitely associated thus far with mass mortalities, but infected chum salmon were found to be more susceptible to vibriosis, less resistant to oxygen depletion, and with decreased osmoregulatory ability (MacMillan et al. 1980). It may well be that the disease has a greater effect on fish populations than was formerly believed.

BLOOD PROTOZOA

In addition to recent attention to the blood disease called Viral Erythrocytic Necrosis (VEN), other blood parasites of fish have been reexamined from the viewpoint of mortality. The hemoflagellate *Trypanoplasma bullocki*, found in a number of marine fishes from the U.S. east coast, has been implicated in extensive mortalities of young-of-the-year summer flounder, *Paralichthys dentatus* (Strout 1965; Daily 1978; Newman 1978; Burreson and Zwerner 1982). Field and experimental evidence suggest that infections are lethal during the colder months of the year. The finding of 100% infection in trawled samples from Chesapeake Bay led to the possibility that the pathogen could have a severe effect on survival of entire year classes of juvenile summer flounder (Burreson and Zwerner 1982).

In other recent studies of hematozoa of fishes, a trypanosome was found in high prevalences (up to 94%) in cod, *Gadus morhua*, from the Canadian Atlantic coast (Kahn et al. 1980). Infestation varied markedly among the stocks of cod sampled.

Another group of blood-inhabiting Protozoa, the haemogregarines, are among the most common of blood parasites of fish. Long considered as benign and widely distributed, their potentially pathogenic role in aquaculture was recently demonstrated (Kirmse 1980). Cultured turbot, *Scophthalmus maximus*, raised at elevated water temperature, were found to be infected with *Haemogregarina sachai*, which caused gross tumorous lesions of the musculature and viscera, in addition to severe blood parasitemias with marked anemia. The lesions were found in up to 6% of cultured populations (Kirmse 1978; Kirmse and Ferguson 1976). This seems to be an excellent example of the potentially pathogenic role which may be assumed in aquaculture by parasites considered benign in wild populations—in which mortalities, debilitation, decreased resistance to other pathogens, and reduced market value may result.

ICHTHYOPHONUS EPIZOOTICS

A pathogen (or pathogen complex) with a remarkable worldwide distribution, in fresh and saltwater, is the systemic fungus parasite *Ichthyophonus hoferi*. It is of interest to us here because of repeated and extensive epizootics in a number of marine species in several parts of the world. New information about the pathogen has been developed in North America and elsewhere. Originally described as a parasite of rainbow trout in Europe (Plehn and Mulsow 1911), it has subsequently been reported in outbreak proportions in mackerel in coastal waters of the British Isles (Sproston 1944); in Atlantic herring on the east coast of North America (Sindermann 1970) and at present in haddock and plaice in waters north of Scotland (McVicar 1980). Furthermore, it has been reported in high prevalence in yellowtail flounder, *Limanda ferruginea*, from the offshore fishing banks of Canada (Powles et al. 1968; Ruggieri et al. 1970), from farmed rainbow trout in Australia (Munday 1976), and from rainbow trout in Japan (Miyazaki and Kubota 1977). Epizootics in cultivated salmonids have been traced repeatedly to use of raw marine fish in diets (Rucker and Gustafson 1953; Munday 1978).

One of the most interesting aspects of this disease is its apparent periodicity—with six recorded epizootics in herring of the western North Atlantic (Fig. 1). The most recent outbreak in herring and mackerel of the Gulf of St. Lawrence occurred in 1954-56, with effects on population abundance that extended well into the 1960's. In its acute form the disease is rapidly fatal, and it was estimated that almost half the spring-spawned herring of the Gulf were destroyed by the epizootic—an estimate that was supported by statistics from the fishery. For the 5-yr period preceding the most recent outbreak, average landings in the southern Gulf of St. Lawrence were 10,800 t; for the 5-yr period immediately following they were only 6,700 t—a decrease of almost 40%, with no apparent change in fishing effort (Fig. 2).

Growth rate increased immediately following the mortalities, and larval abundance declined drastically. Some recovery was noted beginning in 1960-61 (Tibbo and Graham 1963), and longer term effects on herring stocks have been described recently in the Canadian literature (Parsons and Hodder 1975). Reduction in competition and larval predation seemed to provide conditions favorable for production of good year classes—and the 1958 and 1959 year classes were very strong. Abundance of these two year classes as juveniles from 1959-62 and as adults in 1963-68 may have contributed to poor survival of young for almost a decade.

In this example of environmental stress from epizootic disease can be seen a mechanism which tends to increase the amplitude of population fluctuations—positively as well as negatively—and even to provide some clues about stock recruitment. Man's inter-

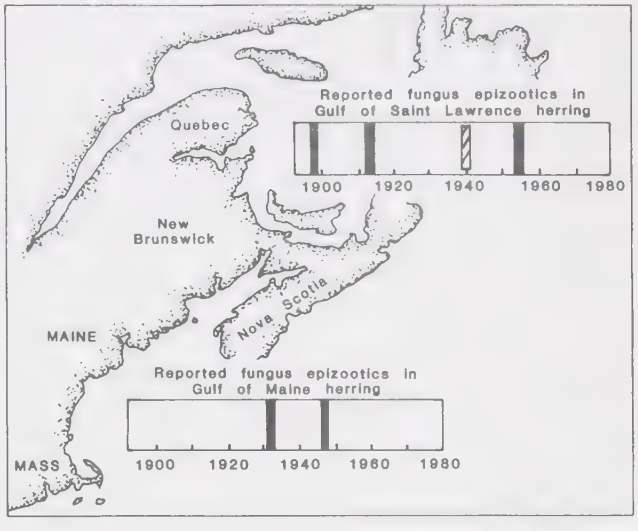

Figure 1.—Reported epizootics of *Ichthyophonus hoferi* in herring of the western North Atlantic. The 1940 outbreak is included on the basis of newspaper accounts only.

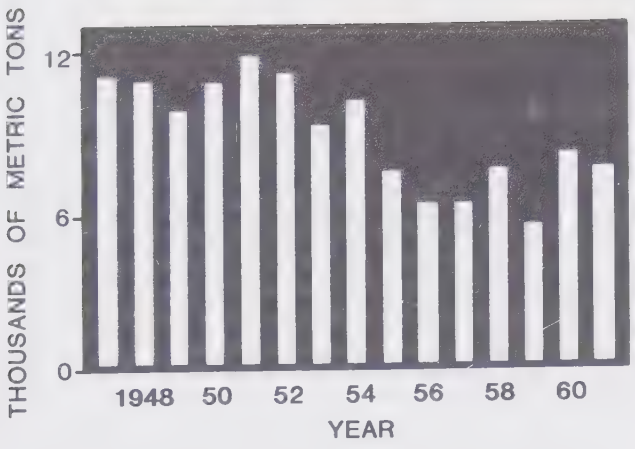

Figure 2.—Herring landings in the southern Gulf of St. Lawrence.

vention here, if any, may have been a positive one—to reduce population size by overfishing beginning in the mid-1960's (Fig. 3), thereby reducing density-dependent factors which increase vulnerability of the population to future epizootics. It is possible that outbreaks may actually be delayed by this mechanism.

The most recent *Ichthyophonus* outbreak—in haddock, *Melanogrammus aeglefinus*, and plaice (*Pleuronectes platessa*)—occurred and still persists in waters north of Scotland. Presence of the fungus was noted as early as 1971; prevalences in haddock from 1976 to 1980 reached 85% in some samples. Prevalences were lower in plaice, not exceeding 25%, but the disease was considered terminal in that species because of the acute nature of the infection and inefficient host responses. Effects of infection, in addition to mortality, include spoilage and decay of flesh of heavily infected haddock, and often extreme emaciation and jellylike flesh of infected plaice (McVicar 1980).

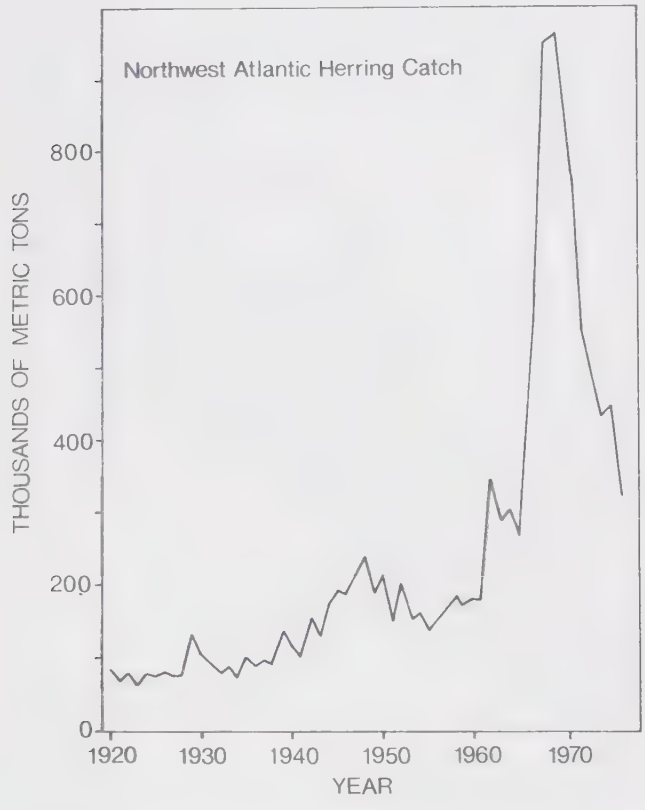

Figure 3.—Recent trends in herring catches in the western North Atlantic.

POLLUTION-ASSOCIATED DISEASES

The important and timely matter of pollution-associated diseases of marine fish can be discussed in five categories: 1) Disease caused by facultative pathogens: Fin erosion and ulcers; 2) stress-provoked latent infections: Shrimp baculovirus, oyster herpes virus, herpes-virus disease of turbot, and lymphocystis; 3) environmentally induced abnormalities: Neoplasms and skeletal anomalies; 4) genetic abnormalities: Egg and larval genetic damage; and 5) experimentally induced lesions. Each of these categories can be examined here very briefly, with examples drawn in part from our ocean pollution research in the western North Atlantic.

Disease Caused by Facultative Pathogens

Our best candidate in this category is fin erosion or "fin rot" of fish, which is probably the best known but least understood disease syndrome of fish from polluted waters. It has been found in the New York Bight, the California coast, Puget Sound, Biscayne Bay, Escambia Bay, Irish Sea, Tokyo Bay, and the French coast. It occurs in two types: 1) Site-specific—especially in demersal fish; probably from contact with contaminated sediments; and 2) generalized—found especially in pelagic fish; with involvement of all fins but especially the caudal; occasional bacterial infections are found.

In the New York Bight, fin erosion has been found in 22 species of fish, and has been demonstrated in flounders to be statistically more abundant in that highly polluted zone than in other comparable coastal areas. It has a statistical association with high coliform and high heavy metal levels in sediments.

In another U.S. coastal area, southern California, fin rot has been found in many species, and is clearly associated with proximity to ocean outfalls of sewage systems. Wherever studied, fin rot disease signs include: Epidermal hyperplasia, dermal fibrosis, hyperemia, occasional hemorrhage, no consistent bacterial infection, and no pronounced inflammatory response.

The possible role of environmental chemical contamination in the etiology of fin erosion emerges more clearly as additional studies are reported. Fish from the New York Bight, reported in studies by Mahoney et al. (1973), Murchelano (1975), and Ziskowski and Murchelano (1975), exist in a highly contaminated area, with chemicals such as heavy metals and petroleum residues in sediments far above background levels. McDermott and Sherwood (1975) in California found DDT to be significantly higher in fish with fin erosion, and PCB levels slightly higher in such fish than in normal individuals. Wellings et al. (1976) found abnormally high concentrations of PCB in English sole and starry flounders with fin rot from the Duwamish River in Washington.

Several authors have postulated that fin erosion in flatfish may be initiated by direct contact of tissues with contaminated sediments. Mearns and Sherwood (1974), for example, suggested that toxic substances (sulfides, heavy metals, chlorinated hydrocarbons, etc.) could remove or modify the protective mucus coat and expose epithelial tissues to the chemicals. Sherwood and Bendele (1975) reported that Dover sole from California with fin erosion produced much less mucus than normal fish.

It seems quite likely that the "fin erosion" syndrome in fish includes chemical stress, probably acting on mucus and epithelium;

stress resulting from marginal dissolved oxygen concentrations, possibly enhanced by a sulfide-rich environment; and, secondary bacterial invasion in at least some instances.

A second disease possibly related to pollution and effects of facultative pathogens is ulcer disease—which is, next to fin erosion, probably the commonest abnormality in fish from polluted waters. It appears to be usually of bacterial etiology. Systemic infections with *V. anguillarum* have been associated with ulcers in New England and Europe. Last year, at a special meeting on diseases of marine fish and shellfish held in Copenhagen, ulcer disease of cod was described from Denmark, the Irish Sea, and the northern coast of France—associated with areas of severe pollution. *Vibrio anguillarum* was the most common isolate, but Danish workers have also identified two viruses in ulcerated fish.

Beginning in 1979, pathologists at our laboratory in New Jersey have recognized an ulcer disease of red hake, *Urophycis chuss*. The disease appears soon after the late winter inshore migration of that species (Murchelano and Ziskowski 1979).

So, for this first category, diseases caused by facultative pathogens, there is much room available for study at the boundary between infectious and noninfectious diseases. This is the area where environmental stress and facultative microorganisms are important; where high bacterial populations in eutrophic waters interact with exposed or injured or chemically modified surface membranes; and where nonspecific pathologies such as fin rot and ulcers can occur in epizootic proportions.

Stress-Provoked Latent Infections

It is generally recognized that certain salmonid diseases in freshwater—such as kidney disease and furunculosis in latent or carrier states—may be provoked into patency by environmental stress. Recent work suggests that latent infections in marine species may be provoked into patency by pollutant stress. We have found, for example, that lymphocystis disease of striped bass, *Morone americanus*—normally a rare disease in natural populations—can occur in high prevalences (up to 25%) in fish overwintering in heated effluents of electric generating stations (Sindermann 1979). Also, a disease caused by a herpes-type virus was reported from turbot in Scotland in 1978. The flatfish were being raised in a fish farm using warmed seawater from a nuclear power plant. One-year-old fish died in large numbers from the disease. Viral arrays were seen in wild fish, but not mortalities—suggesting that the infections were enzootic and latent in the wild turbot population.

Additionally, another herpes-type virus has been found to cause mortalities in oysters on the New England coast, and a baculovirus produced experimental mortalities in penaeid shrimp of the Gulf of Mexico when exposed to PCB's. The conclusion must be that pollutant stress can give us very important clues about the role of carrier states and later infections in the epizootiology of marine diseases.

Environmentally Induced Abnormalities—Neoplasms and Skeletal Anomalies

We have at least 40 yr of circumstantial evidence—beginning with Schlumberger and Lucke's (1948) description of catfish epitheliomas in grossly polluted rivers, through the spread of cauliflower disease (Blumenkohlkrankheit) of eels in northern Europe since the 1950's, and the extensive work with flatfish of the Pacific coast of North America (Stich et al. 1977)—for a possible relationship of fish neoplasms and environmental pollution. An extensive literature has been developed in the United States and elsewhere, but a direct causal relationship has not been demonstrated.

Skeletal anomalies, particularly those of the spinal column of fishes, are the subject of an extensive literature. Included are spinal flexures and compressions, vertebral fusions, and head and fin anomalies. Recent studies in California have reported increased prevalences of skeletal deformities, considered to be pollution related. Valentine (1975) presented the most convincing evidence for environmental influences on induction of abnormalities in three species of fish from the southern California and Baja California coasts. He found significantly higher prevalences of skeletal anomalies, especially gill raker deformities, from Los Angeles and San Diego than from Baja. He suggested a relationship with high heavy metal and chlorinated hydrocarbon levels in California, but stopped short of stating a direct causal relationship.

Genetic Abnormalities

The mutagenic properties of a number of chemical contaminants, including pesticides and heavy metals, have been demonstrated in experimental studies with terrestrial animals. Recent work suggests high percentages of chromosomal anomalies and high prevalence of dead fish eggs in polluted areas of the New York Bight (Longwell 1976). All degrees of chromosomal damage have been found, and higher percentages of anomalies seem associated statistically with the degree of environmental degradation. It may well be that a new and significant mortality factor— increased genetic damage—may have been introduced with increasing chemical pollution. These genetic disturbances fall clearly within the definition of disease.

Experimentally Induced Lesions

There is a vast and almost unmanageable literature about induced lesions in fish after experimental exposure to chemical contaminants. Fortunately, a number of good reviews are available on pathological effects of heavy metals, pesticides, and petroleum. Some generalizations that may be drawn are:

Increasing dosages, beyond a threshold, produce increasingly severe tissue abnormalities;

particular contaminants often exert effects on specific target tissues, but specific lesions cannot usually be described as characteristic of any group or class of chemicals;

much histopathology is nonspecific response to stress or infection;

effects that may be of chemical origin may be obscured by stress-provoked infections with facultative pathogens; and

principal target tissues and organs seem to be gills, liver (or invertebrate hepatopancreas), and neurosensory cells.

Much experimental evidence exists, but it has numerous flaws:

Dosage levels are often beyond maximum observed environmental levels;

usually single chemicals are tested, ignoring synergisms and antagonisms;

often the tests are static acute and not chronic flow-through; and

experimental animals are often under stress from the mere act

of confinement—they may be injured, sick, or dying at the beginning of the experiment.

These and other flaws reduce some of the value of the experimental evidence, but a great pool of such information exists and is of value because of its volume.

It is, of course, necessary to be conservative in conclusions about associations of pollution and disease, but evidence for such associations is increasing.

SOME EMERGING CONCEPTS IN MARINE FISH PATHOLOGY

Disease is a significant factor in survival of fish and shellfish. Information about the role of pathogens in marine populations is accumulating at an accelerating rate. Among the emerging concepts in marine pathology are the following:

1) The effects of parasites and diseases on marine fishes are quantifiable. In those few instances where quantitative studies of disease-caused mortalities have been made (such as the examination of *Ichthyophonus* epizootics) significant reductions in population size have been observed or inferred.

2) Some of the diseases of salmonids, such as furunculosis and bacterial kidney disease, long considered as problems in freshwater hatcheries, are emerging as problems and causes of mortality during marine phases of host life cycles. Conversely, vibriosis, characteristically a marine problem, can be transported to freshwater by species such as eels.

3) Virus diseases, in latent or patent form, have been identified in marine fish, particularly during the past decade. Some of them, such as lymphocystis and eel stomatopapilloma seem relatively benign, while others, such as the IPN-like virus of menhaden, are lethal to the host.

4) Studies of diseases in marine aquaculture have shown that some parasites, such as the haemogregarines, long considered benign, must be reassessed as potential pathogens and causes of mortalities.

5) In considering pollution-associated diseases of fish the following conclusions seem warranted:

a) The significance of environmental stress from pollutants is emerging as a possible determining factor in a number of fish diseases. This may take the form of direct chemical-physical damage to cell membranes or tissues, modification of biochemical reactions, and buildup of facultative microbial pathogens.

b) Some circumstantial evidence for the role of environmental carcinogens in inducing neoplasms of fish and shellfish is accumulating, and is suggestive, but definitive conclusions are not justified at present.

c) The presence of marginal or degraded estuarine/coastal environments may be signalled by the appearance of fin erosion, ulcers, lymphocystis, and skeletal anomalies in teleost fishes. A clear cause and effect relationship has not yet been demonstrated in every instance, but some statistical associations have been made.

d) A number of viruses have been found in fish, crustaceans, and mollusks within the past decade, and the pathogenic role of a number of them has been demonstrated by increasing environmental stress. It may well be that other latent virus infections will be identified by similar experimental methods.

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Applied and Scientific Aspects of Marine Parasitology

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Parasitism is widely distributed among marine animals. At present about 15,000 species of parasitic organisms are reported from marine ecosystems. But even the most understated calculation shows that on the average not more than 25% of living marine parasite species have been described. Practically all species of free-living marine animals are also involved in parasitism, serving as hosts of the appropriate stages of parasites from different systematic groups.

The parasite fauna of marine fishes and invertebrates is extremely rich and diverse and has the largest total biomass. This is primarily due to the numerous helminth larvae (which usually have wide specificity) and the peculiar and very rich fauna of parasitic copepods and isopods (Table 1). Many dozens of species of parasites are usually reported from those fish species which have been extensively studied by parasitologists. Numbers of parasites per host individual in fishes, and especially in marine mammals, may reach hundreds of thousands or even millions. Many parasites are highly pathogenic to their hosts. They can cause diseases and affect the population sizes of marine animals. The role of parasites in natural marine ecosystems is undoubtedly very important. Besides, as is generally known, some marine parasites can be dangerous for human health. Ultimately, the immensity of the seas and oceans; the great diversity of the ecological conditions due to the wide range of abiotic and biotic factors (such as temperature, depth, movement of the water masses etc., the abundance of marine vertebrates and invertebrates and their parasites, and the great biocenotic diversity); the numerous food species of marine invertebrates and vertebrates, often with very abundant stocks; the highly developed coastal and offshore fisheries; and, hence, the huge economic losses [which can be] caused by parasites—all these features of applied marine parasitology provide a boundless field for diverse trends of applied and fundamental investigations.

Table 1.—Approximate number of species in some main groups of parasites of marine animals.[1]

Systematic group of parasites	Number of species described to date	Probable number of living species
Trematodes	3,000	15,000-30,000
Monogeneans	2,200	9,900-13,000
Cestodes	800	2,000- 2,500
Nematodes	500	1,500- 2,000
Acanthocephalans	200	300- 500
Parasitic copepods	2,500	2,500-28,000
Parasitic isopods	900	2,000- 3,000

[1]Calculations were made by Manter (1966) on trematodes [digeneans], Lebedev (in litt.) on monogeneans, and Kazachenko (in litt.) on parasitic copepods of marine fishes.

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The principal trends of the development of marine parasitology (as in any other branch of the science) are determined, on the one hand, by the volume and level of knowledge accumulated in the field and prospects based upon it. On the other hand they depend on the development of research techniques, the general development of adjacent scientific fields and, especially, on today's urgent needs of industry. In marine parasitology such practical requirements arise from the experience and prospects of the marine fisheries.

Taking into account available data on the above-mentioned conditions, I shall try to review the most important and promising directions of applied marine parasitological investigations and some of the fundamental scientific aspects involved.

One must bear in mind that the volume and content of applied branches of aquatic parasitology are very different depending upon the aquacultural, natural freshwater, and natural seawater conditions. Each of these three branches has its own problems, its own strictly definite possibilities, and its own methodology (Kurochkin 1979a). In this paper I shall discuss the applied and scientific aspects of marine parasitology itself, giving no attention to the problems of parasitology in mariculture.

Marine aquacultural parasitology, of course, is a very important branch of marine parasitology and it needs special consideration. However, marine aquaculture in our country has not yet reached the necessary level of development, and problems of control of diseases of cultured marine animals are not so acute for us as compared with some other countries. It is a future problem for us (though we are working on it now). Today's most important applied and, accordingly, scientific problems of marine parasitology are not in the field of parasitology of the few marine fish and invertebrate species under culture. Rather they are in the subject of parasitology of the mass of commercial and the trophically important noncommercial species of animals of the natural marine ecosystems connected with them.

I must add here that in natural marine ecosystems, contrary to marine aquaculture, it is not the objects of microbiology (i.e., viruses, bacteria, and fungi) but the multicellular (helminths, parasitic crustaceans, and some protozoan parasites) that are of the greatest practical importance. The direct economic losses in these cases are not caused by the diseases themselves (as a factor reducing the abundance of commercial animals) but by the parasites which damage the food and its technical qualities and thereby reduce the marketability of commercial marine fishes and invertebrates. Practically speaking there is no possibility (at least for the present) of employing therapeutic or prophylactic methods to control diseases and parasites in natural marine ecosystems (in contrast to marine aquaculture). Here we must use quite different methods to reduce economic losses.

Based upon our experiences, I shall consider below the most significant principal directions [problem areas] of applied marine parasitology and the fundamental aspects directly connected with them. Six principal directions [problem areas] are enumerated below:

1. The correct determination of the taxonomic (specific) position of parasites.

Unfortunately, the importance or significance of this thesis sometimes still needs to be proved (Willmott 1976), but it is quite impossible to carry out any applied or fundamental investigations or to accomplish any practical measures without an exact identification of the parasites involved.

In marine parasitology, identification of the parasites is especially important and often is connected with certain specific difficulties. Here, unlike medical and veterinary parasitology (and the parasitology of freshwater aquaculture), only a relatively small portion of living parasite species (probably from 10 to 60% in general systematic groups) are known at this point. The number of species of marine parasites, as already stated, is extremely great, but their systematics is still imperfect. In treating parasitological collections one often has to describe new species of parasites or create new taxa of higher rank. At times economically important parasites appear to be new species. An example is the copepod *Pennella hawaiiensis* Kazachenko and Kurochkin, 1974, affecting the commercial fish *Pentaceros richardsoni*. (Some information on this case will be given below.) Another example is the trematode *Gonocerca oshoro* Shimazu, 1970, which was originally described by Shimazu (1970) from a few specimens of trematodes from a single fish. Parasitologists of TINRO soon discovered that these trematodes are often found in the ovaries of their fish hosts (*Coryphaenoides pectoralis*) in great numbers. As a result the hard roe of parasitized fish becomes inedible and has to be discarded. Obviously, this trematode, *Gonocerca oshoro*, may also have adverse effects on the reproduction of the host.

Often it becomes necessary to identify not only mature parasites but also their larval stages, of which only their remains or even traces may persist. We (Kurochkin 1969; Kazachenko and Kurochkin 1974) have described a case where the marketing of commercial catches of the fish *Pentaceros richardsoni* was temporarily prohibited until the origin of [obvious] dark formations in the muscles of the fishes was identified. First, the marketing of 36,000 tons of this fish was delayed, then as many as 133,000 tons. It is clear that the economic losses due to the delay of the marketing of such a large amount of fish (even if one takes into consideration only the cost of the electrical energy spent for the freezer storage of this quantity of fish) are rather high. The ban was removed only after some months, after our parasitologists had found and proved that the above-mentioned dark formations in fish muscles are the remains and traces of a new copepod species (*Pennella hawaiiensis*) which is not dangerous to man.

Correct determinations of the taxonomic position of parasites and, in particular, the elaboration of specific methods of identifying them, as is necessary for the fisheries, are impossible without further development of a certain complex of fundamental trends of marine parasitology. Primarily, I mean the systematics and taxonomy (with nomenclature) based on morphology (where studying the individual, age, hostal and geographical variability of parasites is especially important) and then corresponding aspects of the ecology, biology, physiology, and biochemistry of parasites and some aspects of their phylogeny. Preparation and publication of systematic catalogues and monographs and keys for the determination of different groups of parasites are also of great practical importance.

2. Studies of the spatial distribution of the infection of marine commercial animals by important species of parasites, with due regard for the age, seasonal and long-term quantitative and qualitative changes.

This complex of investigations provides the parasitological characteristics of the commercial marine animals and fishing areas. These characteristics, if sufficiently complete and detailed, allow, in many cases, the planning beforehand of the proper kind of processing of the catches which otherwise could not be utilized properly because of high infestation by certain parasites. Sometimes it becomes possible for us to avoid significant economic losses by not sending the fishing vessels to those areas where catches could not be utilized properly because of high infestation by certain parasites. Of course, parasitological investigations concerning new commercial species or new fishing areas must be accomplished ahead of the development of a commercial fishery. But the accumulation of parasitological data in well-exploited fishing areas over many years has to be accomplished also, by means of necropsies of large numbers of fishes obtained from commercial fishing vessels.

It takes parasitologists a long time and much trouble to collect the materials and data necessary for the above-mentioned purposes, and it is almost impossible to do so without special research vessels. For example, the Laboratory of Parasitology of Sea Animals of the Pacific Research Institute of Fisheries and Oceanography (TINRO), Valdivostok, U.S.S.R., (as well as other laboratories of this Institute) has a large research fleet at its disposal. During the 15 yr of the existence of this laboratory (1966 to 1981) its parasitologists have employed the research vessels of the Institute heavily. The duration of these expeditions totals up to more than 36 yr! More than 70,000 fishes, 500,000 invertebrates, and 6,000 marine mammals were dissected by parasitologists, who also carried out some experimental investigations. Besides, a large number of fresh and frozen marine fishes and invertebrates were studied by our parasitologists during numerous coastal parasitological expeditions and in the laboratory in Vladivostok. Our investigations in the direction [problem area] under discussion have often yielded good practical results. For example, the utilization of our proposals based on the above-mentioned investigations, regarding only the Alaska pollock, *Theragra chalcogramma*, in 1977 allowed our fishing industry to produce an additional 200,000 tons of food (Kirillova et al. 1979). As a result of our work during the last 5 yr, our country has received over 1.5 million tons extra of food production from Alaska pollock.

To develop this, one of the most important directions [problem areas] of applied marine parasitology, it is useful and necessary to develop a certain complex of fundamental investigations with the main purpose of understanding the general mechanisms and factors governing the spatial distribution of infestation of marine animals by parasites. It is very important to have knowledge of the permissible limits of extrapolation of some parasitological data in this field. It is also necessary for the purpose of developing the ability to forecast future changes in the distribution of infestation and in the quantitative and qualitative indices of invasion. Therefore, the relevant aspects of the parasitofaunistic, ecologicoparasitological, parasitocoenological, and zoogeographical studies as well as investigations in the fields of population biology and population ecology of parasites are of great practical importance.

3. Studies of the distribution of the important parasite species within the bodies of marine fishes and other commercial marine animals.

Here I do not mean the generally accepted registrations [recordings] of the localization [location] of parasites (gills, stomach and intestine, etc.). These data are not very useful for most practical purposes. Usually relatively few species of parasites, mainly from muscles and other edible parts of the host's body, are of practical

interest. In some cases very detailed and reliable statistical information about the topospecificity of these parasites are needed. Obtaining such information demands much labor, especially if we must consider the possibilities of age and seasonal changes in the distribution of parasites.

Data thus obtained allow us to advise on methods of utilization of catches of some fish species or the most suitable kinds of processing for these fishes. Also these data can be used as the basis for working out the rational geometry of dressing-out (cutting) fishes or other commercial animals in order to remove the highest possible number of parasites, or their remains. Sometimes we, ourselves, are able to propose new types of industrial processing based on the data obtained. More often we use our information to check new types of processing proposed by workers of the fishing industry.

To illustrate the practical importance of investigations of this direction [problem area], I shall give some figures of the economical losses which we hope to eliminate using our proposals. Using the rejection of large amounts of tinned saury because of invasion and infections by bright red or orange acanthocephalans of the genus *Rhadinorhynchus* as an example—economic losses due to the discarding of some part of the production at only one of our fish canneries reached the sum of more than a million roubles in 1980.

Of the fundamental investigations immediately connected with the above-mentioned applied direction [problem area] of marine parasitology one can notice, especially, research on parasite topospecificity, investigations of mechanisms of orientation and migration of parasites in the host's body, and certain aspects of parasitocoenology, physiology, and population biology of parasites.

4. Studies of the survival and behavior of parasites in the fish host after death, during storage, and under the influence of various physical and chemical factors.

The main aims of this experimental direction [problem area] of applied marine parasitology are to develop methods and conditions of processing raw fish which guarantee the reliable killing of parasites dangerous to man (e.g., anisakid larvae); to find measures to prevent the wandering of some parasites (e.g., *Nybelinia* larvae) in the fish before it is frozen or processed; and to elaborate measures preventing the spoilage of the fish flesh by certain myxosporidian parasites (e.g., of the genus *Kudoa*) during the storage and after the fish had been frozen and defrosted.

From this point of view it is very important to test new as well as routine methods of fish processing and to check the effects of such factors as temperature, time, salt (NaCl) content, etc.

Results of research by numerous investigators, both in the U.S.S.R. and abroad, have demonstrated the great practical significance of this applied area of marine parasitology.

The fundamental trends of investigations related to these applied works are the experimental ecology of the relevant stages of development of parasites and certain aspects of the physiology of parasites.

5. Studies of the influence of parasites on the quality of raw and processed marine fish and invertebrates.

Parasites can cause different local and general disorders in the host organism. These are manifested in undesirable changes of appearance, structure [texture], flavoring, and other technical qualities of flesh or other tissues of marine commercial animals. These changes are usually registered [detected and recorded] with the help of the organoleptic and laboratory biochemical indices. Studies of the rate of such changes, with due regard for the chemical composition of parasites themselves, constitute an important practical problem. The results of these investigations allow us to decide what kinds of uses are best for certain batches of fish, to develop quantitative criteria for permissible contents of parasites and injuries [parasite damage] in marine food stuffs, and to introduce necessary corrections into the procedures and technology of processing of marine fishes or invertebrates.

Many studies of this direction [problem area] have been carried out in the U.S.S.R. and in other countries, but the area as a whole cannot yet be considered to be well developed.

This applied direction is based on relevant [fundamental] aspects of biochemistry, pathophysiology, pathoanatomy, histopathology, and toxicology.

6. Development and improvement of methods and standards for the parasitological inspection of marine fishes and invertebrates.

The main aim of this practical direction [problem area] of work is prevention of the marketing of marine foodstuffs of poor quality or dangerous for human health (due to parasites) on the one hand and on the other, prevention of unjustified rejection of marine food production which is essentially of good quality. It is rather difficult to achieve both of these mutually exclusive requirements, but, unfortunately, unjustified and erroneous rejections of food fish are not rare, and they cause significant economic losses.

I shall enumerate the most important things that can be done to help avoid or reduce economic losses:

1) Elaboration of standard procedures for the parasitological inspection of fish and other commercial marine animals (including establishment of sample sizes, etc.).
2) Elaboration of fast and reliable methods of detection and calculation of the most important parasites in raw material and in foodstuffs made of marine fishes or invertebrates.
3) Elaboration of express methods for identification of important species and groups of parasites.
4) Elaboration of quantitative criteria and norms for the permissible (or inadmissible) contents of parasites, their remains, or injuries [damage] in different kinds of raw and processed marine fishes and invertebrates.
5) Receiving approval of the appropriate official organizations for the new regulations and standards that have been worked out and introducing them into the State or departmental standards and technological instructions; preparing and publishing various methodological textbooks and manuals, including the handbooks for parasitological inspection of marine fishes and invertebrates, and, finally, performance of the parasitological inspections themselves.

The experience of the Laboratory of Parasitology of Sea Animals of TINRO concerning all of these questions shows that very often it is possible to succeed in reversing (in proper time) [where time allows] erroneous decisions to discard certain batches of marine fish because of the presence of parasites. Such batches often contain several hundred tons of fish, and unjustified rejections cause great economic losses which could be avoided. For example, about a thousand tons of frozen Alaska pollack were discarded without good reasons (because of presence of parasites in the intestine and in the gills, etc.) in 1978. But in many cases we have time to step in and save large amounts of fish of good quality.

The practical importance of reference books and other research publications is illustrated by the fact that two editions of "Methodical handbook for parasitological inspections of marine fishes" (Kurochkin 1980a, b) were published and sold out (based on orders from the fishing industry) within a year.

It is clear that this important direction [problem area] of applied marine parasitology is connected with a large complex of different fundamental studies which were mentioned above when I considered the other applied directions.

The enumerated six main directions [problem areas] of applied marine parasitology are based on the present immediate needs and tasks of our fishing industry. Results of investigations in these areas are not merely of conditional or of indirect practical importance but of real effectiveness, which usually is very high and may be easily estimated in terms of weight or money.

It would be extremely useful for the future development of applied and, therefore, fundamental investigations in marine parasitology if both the general and detailed information on cases and on the scale of economic losses were always estimated and published. Economical losses in this field and the practical (economical) possibilities of applied marine parasitology are much more significant than generally realized. The main purpose of this report is to invite attention to the possibility of avoiding very large economic losses by development of the applied aspects of marine parasitology.

Of course, it will not be possible to forestall [obviate] all manifestations of parasites' ravages. For example, justifiable rejections of highly infested fish are inevitable. Even so, parasitological inspection of such fish performed as soon as possible (not after long-term storage and long transportation) will diminish economic losses.

There are other trends of investigations in marine parasitology which, with good reason, may be considered as applied, though they usually are not of direct applicability. They are:

1) Studies of the medical aspects of the parasitofauna of marine animals (diagnostics, pathogenesis, clinical course of diseases, epidemiology, prophylaxis, etc.).
2) Studies of the diseases caused by parasites and their influence on the populations of marine animals (levels or degrees of mortality, reduction of reproduction, estimation of losses of weight or number of fishes, estimations of reductions in the volume of catches, clinical signs of diseases, etc.).
3) Studies of the infectious (viral, bacterial, and fungal) diseases of marine animals and their role in the natural ecosystems.
4) Studies of the interaction between infectious and invasive diseases of marine animals.
5) Studies of the possibility of using parasites as tags of population structure, migration routes, and some other aspects of the ecology and biology of marine free-living animals.

It is obvious that at least three of the above trends of investigations are of direct practical importance for aquaculture in the marine environment. I shall not dwell upon the subject.

Some other important trends of applied and fundamental investigations in marine parasitology are outlined by Sindermann (1970), Rohde (1976), Llewellyn and Owen (1960), Llewellyn (1972), and others. Very interesting reviews on the problems of fish parasites and of parasite coenoses in fish (with many questions concerning marine parasitology) were published by Bauer (1978, 1980). There are other papers containing considerations of the subject.

Undoubtedly, all aspects of marine parasitology have to be well developed. Among them special attention has to be paid to those applied aspects I have mentioned. Doing so will further the subsequent development of both applied and fundamental investigations in the field.

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Use of Parasitological Data in Studies of the Local Groupings of Rock Grenadier, *Coryphaenoides rupestris* Gunner

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ABSTRACT

The local groupings of rock grenadier in the northwestern, northeastern, and open Atlantic are identified on the basis of parasitological data. It is shown that these are temporary groupings mixing with each other. The problem of interrelation of the fishes under study in different parts of the area is discussed. The pattern of the life cycle of the rock grenadier involves the migration of immature fishes from the southern areas of the northwest Atlantic (Flemish Cap and northern Newfoundland Banks) to the reproductive areas located in the eastern regions of the North Atlantic.

Studying the population structure of certain sea fishes by using parasitological data is not a new subject. It is sufficient to mention the papers of Sindermann (1961), Yanulov (1960, 1962), Templeman (1967), Kabata (1959, 1963, 1967), Schulman (1950, 1956), Konovalov (1971), and others. These papers are not equal in value but they proved the possibility of using parasites to study fishes. True, in all these cases freshwater, diadromous, shelf-dwelling fish and also fish dwelling in the upper pelagic layers, served as the subjects of study. Deepwater fish have not been studied in this respect.

The rock grenadier is a typical bathyal dweller. This species is widespread, being distributed near the coast of North America, from Baffin Island to Cape Hatteras; in the waters around Greenland and Iceland; in the central part of the North Atlantic along the Mid-Atlantic Ridge up to lat. 40°N; on the continental slope of Europe; and near the Scandinavian coast up to the Skagerrak Strait. The biology of this species has been studied only poorly. This species is of especial interest because near the coast of North America only immature fish were found, whereas in the central and eastern parts of the North Atlantic fish of all stages of maturity were captured. It is not clear yet whether there is an interrelation between these groups, though there is a supposition that such relations exist (Zakharov and Mokanu 1970). Such supposition is based on indirect data. Also, a preliminary conclusion based on parasitological data was made on the existence of a common rock grenadier population in the western and central parts of the North Atlantic (Zubchenko 1976). There are data which confirm this supposition (Alekseev et al. 1979), and there also are contrary opinions (Marshall 1965; Galaktionova 1978; Dushchenko 1979).

The first information on parasites of rock grenadier appeared in 1911 when Odhner (1911), using fish which were caught offshore of Norway, described the trematode *Proctophantastes* (=*Steganoderma*) *abyssorum*. Later, Brinkmann (according to Sproston 1946) described the monogeneid *Dactylicotyle* (=*Diclidophora*) *macruri* in fish from the Skagerrak Strait, and Berland (1961) found the nematode *Contracaecum aduncum* in grenadier from the Norwegian Sea. During the last decade study of the parasite fauna of rock grenadier was rather intensive. *Myxidium* sp., *Contracaecum aduncum*, and the cestode, related to the Dibothriocephalidae family, were found in fish from the Norwegian Sea (Nobel et al. 1972). The rock grenadier of the North Atlantic were found to contain *Myxidium coryphaenoidium* (Yoshino and Noble 1973; Moser et al. 1976); *Hemiurus* (= *Glomericirrus*) *macrouri* and *Gonocerca macrouri* (Gaevskaya 1975, 1979); *Myxidium melanostigmum*, *M. melanocetum*, *M.* (*noblei*?), *Myxidium* sp., *Zschokkella hildae*, *Auerbachia pulchra*, *Diclidophora macruri*, *Bothriocephalus* sp., *Scolex pleuronectis* 1., *Aporocotyle simplex*, *Hemiurus macrouri*, *Aponurus argentini*, *Derogenes varicus*, *Gonocerca macrouri*, *Sclerodistomum* sp., *Contracaecum aduncum*, *Anisakis* sp. 1. and Copepoda gen. sp. (Zubchenko 1975, 1976; Zubchenko and Krasin 1980); and *Dolichoenterum* sp., *Gonocerca crassa* (Szuks 1975), and *Paraccacladium jamiesoni* (Bray and Gibson 1977). Considering only those whose diagnoses have been verified, 21 species of parasites are known for the rock grenadier.

Collections of parasites in rock grenadier which were made in 1973-80 on different areas of the North American continental slope, on the Mid-Atlantic Ridge, and on European deepwater banks, such as Bill Bailey's Bank, Lousy Bank, George Bligh Bank, Hatton Bank, and Porcupine Bank, provide the material for the present paper.

Twenty-five species of parasites were found in 1,126 fishes investigated by the method of complete parasitological dissection and examination. (Among those listed above only *Steganoderma abyssorum*, *Dolichoenterum* sp., and *Gonocerca crassa* were not found.) Nine of them (*Myxidium melanostigmum*, *M. melanocetum*, *M.* (*noblei*?), *Auerbachia pulchra*, *Diclidophora macruri*, *Phillobytos atlanticus*, *Glomericirrus macrouri*, *Gonocerca macrouri*, and *Paraccacladium jamiesoni*) are typical for the parasitic fauna of the rock grenadier. It is not ascertained yet to which species such parasites as *Myxidium* sp. and Nematoda gen. sp. belong. The other parasites (*Zschokkella hildae*, *Grillotia erinaceus*, *Scolex pleuronectis* 1., *Pseudophyllidea* gen. sp., *Aporocotyle simplex*, *Lecithophyllum antheroporum*, *Derogenes varicus*, *Gonocerca macroformis*, *Contracaecum aduncum*, *Anisakis* sp. 1., *Echinorhynchus* sp., *Chondracanthus radiatus*, *Lateracanthus quadripedis*, and *Clavella aduncum*) are widespread and have a wide circle of hosts. Invasion [infection] of fish by them is mainly light and has an accidental character. In this group of

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parasites only the copepod *Lateracanthus quadripedis* (previously observed in the Pacific Ocean), is of a proper interest (the very fact of its finding is historically unique). The same is so with the microsporidian *Zschokkella hildae* and the trematodes [digeneids] *Gonocerca macroformis* and *Aporocotyle simplex*. The first two species are typical for Gadidae and the third for plaices. Finding these parasites in the rock grenadier bears witness to the phylogenetic and ecological closeness between fish of the orders Macruriformes, Gadiformes, and Pleuronectiformes.

In any case, the most interesting are the parasites from the first group which are widespread and which, as a consequence, characterize the parasitic fauna of the rock grenadier. In the fish studied offshore of North America—where, as was already mentioned, only immature fish were observed—19 species of parasites were found, 8 of which were related to the first group. Only the trematode [digeneid] *Paraccacladium jamiesoni* was not found. In North Atlantic waters we can identify three main groups of fish based upon differences in the degree of infection of fish by parasites: The northern group—dwelling in the area between the Greenland-Canadian Threshold and the southern edge of Baffin Island; the central group—dwelling in the Labrador area; and the southern group—dwelling in the area of the Grand Newfoundland Bank and the Flemish Cap Bank. (The names of groups are provisional.)

Fish from the northern grouping were not infected by *Myxidium melanocetum* or *Glomericirrus macrouri*, but they were severely infected by *Auerbachia pulchra* (85.3%); moderately by *Myxidium melanostigmum* (38.6%); and weakly by *Gonocerca macrouri* (14.6%) and other parasites. Fish of the southern grouping were infected to a lesser level by *Auerbachia pulchra* (60.0%) but they were more severely infected by *Myxidium melanostigmum* than those in the north (46.6%) and also by *Gonocerca macrouri* (33.3%). In fish of this grouping, spores of *Myxidium melanocetum* were found (16.6%) and also the trematode [digeneid] *Glomericirrus macrouri* (13.3%). Due to its degree of infection the central grouping occupies an intermediate position, so to speak. Just as in fish from the northern region, *Glomericirrus macrouri* were not found in the fish studied from this area. Infection by *Auerbachia pulchra* in these fish appears like that in fish from the southern area, and the infection by *Myxidium melanostigmum* (33.3%) appears like that in the northern area fish. Spores of *Myxidium melanocetum* were also found in a small number (4.4%), just as in the south.

While investigating rock grenadier from these areas I learned that infection by *Auerbachia pulchra* is the most severe in the northern areas (from 73.3 up to 100%) and especially in fish having lengths of from 42 to 70 cm, which are heavily invaded. To the south where the fish infected by *Auerbachia pulchra* had an average length of 65-85 cm, the invasion was less severe. Mainly sporadic [occasional] spores were found in this case while tens and hundreds of spores were observed under the microscope very rarely.

In fish invaded by the trematode [digeneid] *Gonocerca macrouri*, and the myxosporidian *Myxidium melanostigmum*, the picture was just the contrary. Here the infection of fish increased in the direction from north to south. In this case big fish (from 65 cm and longer) were infected most severely. As was mentioned above, fish in the southern areas were invaded by *Myxidium melanocetum* and *Glomericirrus macrouri* which were not found in fish of the northern grouping.

At first sight, all these differences have an age character which relates first and foremost to the parasite's developing with the change of intermediate hosts. But having taken duplicate samples, first after 1 to 1.5 mo and then in a year, there were no changes in the degree of infection of fish of the northern grouping by the principal parasites, except that they were infected by the cestode *Phillobytos atlanticus* to a lesser degree (from 40 to 13.3%). Similar changes were observed in fish from the central and southern groupings. Besides, the fish had a decreased incidence of attacks by Microsporidae. For example, invasion by *Auerbachia pulchra* decreased from 60 to 40% and their invasion by *Phillobytos atlanticus* increased from 13.3 to 33.3%. These facts testify that the differences observed in the distribution of parasites are not related only to age. The changes observed in the quantitative indices of invasion of fish by a group of parasites during short periods of time are connected, in my opinion, with the migration of the fish (as they grow) from the northern areas to the southern ones. This supposition is confirmed indirectly by the fact that fish from the southern grouping are, in general, larger (mode 69-74 cm) than those from the northern groupings (mode 63-65 cm). The great number of parasites common to these three areas (75%) also indicates connections between these groups.

Studies of fish from the open part of the North Atlantic disclosed 17 species of parasites, among which are all of the 9 species characteristic for rock grenadier. According to the differences in infection of the fish by those nine species of parasites (just as offshore of North America), we may identify three main groups of fish: The northern—dwelling between Iceland and the middle part of the Reykjanes Ridge; the central—dwelling close to the southern part of this ridge; and the southern—dwelling in the northern waters of the North Atlantic Ridge (all the names of the groups are conditional), but these differences are expressed rather slightly.

The trematode [digeneid] *Glomericirrus macrouri* was not found in the rock grenadiers of the northern group, but they were invaded [infected] slightly by the microsporidians *Myxidium melanostigmum* (24.2%) and *Auerbachia pulchra* (29.3%). The fish were infected more severely by the trematode [digeneid] *Paraccacladium jamiesoni* (37.4%). Fish of the central group (like those of the northern group) were not infected by *Glomericirrus macrouri*, also. But fish of the central group were infected to a lesser degree by *Myxidium melanostigmum* (18.9%), *Auerbachia pulchra* (14.9%), and *Paraccacladium jamiesoni* (12.3%) than those in the north. In the southern areas, specimens of *Glomericirrus macrouri* were found only rarely. But the fish there were infected by *Myxidium melanostigmum* (30.2%) and, more severely, by *Auerbachia pulchra* (34.8%). Fish of the southern group were infected by *Paraccacladium jamiesoni* more heavily than those of the central group.

Analysis of my data disclosed that the degree of fish infected by the principal parasites varied significantly during the different periods covered by the investigation. Thus, during the winter period fish of the northern group were infected severely by *Paraccacladium jamiesoni* (33.3-53.3%) and slightly by *Auerbachia pulchra* (6.6-13.3%). In fish of the central and southern groups, *Paraccacladium jamiesoni* was not found at all and the degree of their invasion by *Auerbachia pulchra* was very low (6.6-20.0% and 6.6-13.3%, respectively). In April the infection of the northern rock grenadier group by *Paraccacladium jamiesoni* decreased to 13.3% and then gradually increased to 25.0% in May and 50.0-58.3% in June-August. In April the degree of infection of fish of the central and southern groups by this trematode increased abruptly (38.5% and 50.0%, respectively). Afterwards, in the central area it decreased to 12.5-13.0% (May to July) and again increased in August to September up to 20.0-33.3%. Invasion of

fish of the northern grouping by *Auerbachia pulchra* during the period April to August was very low (13.3-23.6%) and it increased only in September (33.3%).

The picture in the two other groups of fish infected by this microsporidian was quite different. Invasion of fish from the central grouping increased sharply in April (46.6%). It decreased in the period May to August (20.0-12.5%) and again increased in September (46.6%). During almost all this period, fish from the southern grouping were severely invaded by *Auerbachia pulchra* and only in September did the degree of infection decrease to 33.3%. Other quantitative and qualitative changes were observed during our investigations. So, in April and May the microsporidian *Myxidium melanocetum* disappeared from the northern grouping of fish and the cestode *Phillobytos atlanticus*, not observed in winter, appeared (3.6%). Incidence of infection by the monogenean *Diclidophora macruri* decreased (10.8%). But in June, fish of this grouping became infected by *Myxidium melanocetum* (8.3%), while the percentage of fish invaded by *Diclidophora macruri* increased (33.2%) and in July to August the initial picture of the infection was restored approximately, except for an increased infection by *Phillobytos atlanticus* (25%). Noticeable quantitative and qualitative changes took place also in the two other groupings. These changes coincided with the maximal spawning activity of the rock grenadier also.

The facts presented testify that an interconnection exists between the groupings of rock grenadier dwelling on the Mid-Atlantic Ridge, and the nature of the changes in infection of fish indicates that fish from the northern areas migrate south to the spawning grounds where all the groupings mix with each other. After spawning, the fish migrate back to the feeding areas, which is confirmed by the restoration of the initial picture of infection.

On the deepwater banks of the European continental slope where 19 species of parasites, including all the main species, were found in rock grenadiers, quantitative and qualitative changes also were observed which allow delineation of three groupings of fish. The first grouping dwells in the area of the Bill Bailey's and Lousy Banks. The microsporidian *Myxidium* (*noblei*?) was not found in fish of that grouping, nevertheless they were heavily infected by the microsporidian *Auerbachia pulchra* (46.6%) and the monogenean *Diclidophora macruri* (46.6%), and slightly infected by the microsporidians *Myxidium melanostigmum* (26.6%) and *Myxidium melanocetum* (22.2%). Infection by other parasites was very low and did not exceed 13.3%. The trematode [digeneid] *Paraccacladium jamiesoni* was not found in fish of the second grouping, dwelling on the northern part of Hatton Bank and on George Bligh Bank. Though fish of that grouping were quite heavily infected by *Myxidium melanostigmum* (50.0%) and *Auerbachia pulchra* (40.0%), invasion by *Myxidium melanocetum* was less severe (33.3%). Invasion by other species of parasites was slight. The third grouping of fish is distinguished by the absence of the cestode *Phillobytos atlanticus*. Nevertheless, it is heavily infected by *Auerbachia pulchra* and less infected by *Myxidium melanostigmum* (33.3%) and *Myxidium melanocetum* (33.3%). This grouping dwells on the southern part of Hatton Bank and on Porcupine Bank. This particular grouping had the most permanent characteristics in winter when duplicated investigations did not expose [disclose] any substantial qualitative and quantitative changes of the parasitic fauna. Such changes were marked in summer when the percentage of fish of the first grouping infected by *Paraccacladium jamiesoni* increased abruptly (53.3%). Invasion of the fish by other parasites was almost unchanged.

In fish of the second grouping, infection by *Myxidium melanostigmum* and *M. melanocetum* increased still more (73.3 and 66.6%, respectively). Infection by *Auerbachia pulchra* decreased (20.0%), and the trematode [digeneid] *Paraccacladium jamiesoni* —not observed earlier—appeared.

In fish of the third grouping, infection by *Myxidium melanostigmum* and *M. melanocetum* also increased up to 93.3% and 53.3%, respectively, and the cestode *Phillobytos atlanticus* also appeared. In my opinion, the changes in the parasitic fauna of the rock grenadier, which were identified in the summer period, indicate an interconnection of the fishes from different groupings.

The intermingling of fish from neighboring groupings as well as a considerable increase in the percentage of fish infected by *Myxidium melanostigmum*, *M. melanocetum*, and *Paraccacladium jamiesoni*, and the appearance of *Phillobytos atlanticus* testify that fish from the central part of the North Atlantic, where a high degree of infection by these parasites was observed, migrate to the European coast.

But this is not the only fact indicating the existence of an interconnection between the rock grenadier groupings which dwell on the European continental slope, on the Mid-Atlantic Ridge, and along the coast of North America. While studying the parasitic fauna of fish collected in these areas I learned that of the 25 species of parasites discovered, 15 species (60%) may be found in all of the above mentioned areas. Among these parasites eight of nine (88.9%) are common and characteristic for rock grenadier. For example, if we compare the parasite faunas of the northern grenadier, *Macrurus berglax*, studied in the same areas, only 4 of 26 species (15.4%) were common—3 of them are widespread and only 1 species (*Auerbachia pulchra*) is characteristic for Macrouridae.

Infection of the rock grenadier by this species is very peculiar and interesting. In the Mid-Atlantic Ridge area and offshore Europe, fish of larger size (63-104 cm) are infected by *Auerbachia pulchra* more severely than those offshore of North America (55-73 cm). Additionally, the most severe infections in the first two areas occur in fish from 70 to 95 cm long. About 80.0% of fish infected by that microsporidian are distributed in the southern areas, i.e., those areas where fish of different groupings were mixed (as was mentioned above). Offshore of North America, fish of the northern grouping are severely infected by this parasite (85.3%). The invasion [infection] decreases to the south but, nevertheless, remains high enough (48.8-60%). Exactly the same picture may be observed in fish dwelling on the continental slope of Europe. But, on the contrary, infection by *Auerbachia pulchra* in fish of the Mid-Atlantic Ridge decreases from south to north. Additionally, it is peculiar that in this area the percentage of infected fish does not exceed 6.6 to 20.0% during the winter period, but in summer the number of infected fish increases and reaches 57.1% in August. Minimal invasion (13.3-20.0%) by *Auerbachia pulchra* in fish dwelling on the continental slope of Europe is observed in summer, and in winter the percentage of infected fish substantially increases and reaches 53.3% in the northern part of the area. We relate the fluctuations in rock grenadier infection by *Auerbachia pulchra* to the fact that rock grenadier from offshore of North America, where the level of infection by this microsporidian is constant and high, migrate to the southern areas of the Mid-Atlantic Ridge and also to the northern areas of the continental slope of Europe.

The observed regularities in rock grenadier invasion [infection] by the cestode *Phillobytos atlanticus* support this supposition. In the summer of 1973, 14.9% of dissected and examined fish from the Mid-Atlantic Ridge were invaded by this parasite. Worms of from 4 to 10 cm long, with well-developed sexual complexes, were found in the fish. In a year, *Phillobytos atlanticus* were not

found in fish of this area but were found in rock grenadier (19.8%) caught in the North Newfoundland Bank area. The length of the worms was 2-3 cm and their sexual complexes were poorly developed. In the winter of 1974-75, *Phillobytos atlanticus* were found in 15.3% of fish captured offshore of North America. These were very young worms, having lengths of from 2 mm to 1 cm. At the same time the percentage of fish infected by this cestode decreased to 6.6% in the area of the North Newfoundland Bank, where it usually fluctuated between 19.8 and 33.3%. Finally, during the summer of 1975, *Phillobytos atlanticus* were found in fish dwelling on the Mid-Atlantic Ridge. A quite similar picture was observed in 1976-77, in 1978-79, and in 1979-80 in the southern areas of Hatton Bank. Disappearance and appearance of *Phillobytos atlanticus* in rock grenadier from the eastern areas of the North Atlantic are evidently cyclic in nature. It should be added that cyclic recurrence is observed also in infections of fish by *Auerbachia pulchra*.

From these findings we may suppose that rock grenadier migrations from the coast of North America have a 2-yr cycle, apparently. The fact that during some years fish of the eastern areas were not infected by *Phillobytos atlanticus* indicates that the main breeding ground of invasion by this cestode is in the North Atlantic and the parasite is brought to the Mid-Atlantic Ridge by migrating fish. The same thing relates also to the microsporidian *Myxidium* (*noblei*?) infection which decreases from west to east. According to the data of Gaevskaya (1979), exactly the same picture is observed in fish infected by *Glomericirrus macrouri*.

Thus, the results obtained allowed us to discover that in the areas investigated the rock grenadier forms local groupings [populations] which mix with each other during certain periods. The peculiarities of rock grenadier distribution and differences in their invasion by *Auerbachia pulchra* and *Phillobytos atlanticus*, and by some other parasites, show the interrelation between fish dwelling near the coast of North America, on the Mid-Atlantic Ridge, and on the continental slope of Europe. Considering these data, the scheme of rock grenadier migrations proposed earlier (Zubchenko 1976) should be clarified or modified as follows: Rock grenadier larvae are carried by the North Atlantic Current to the northern areas of the Ridge where some of the larvae settle. The rest reach Davis Strait with the western branch of the Current and there become distributed along the Canadian coast. As the rock grenadier [individuals] grow, they move to the Grand Newfoundland Bank and Flemish Cap Bank whence they migrate to the Mid-Atlantic Ridge and Hatton Bank areas where their main spawning grounds are situated. Two spawning areas may be identified on the Mid-Atlantic Ridge, the southern area, where fish from the Canadian coast spawn, and the northern one, where the main part of the grouping consists of repeat spawners. Also there are reasons to suppose that fish from the northern areas of the Mid-Atlantic Ridge migrate to the European banks areas. Spawned-out fish do not return to the Canadian coast, but remain in the eastern areas of the North Atlantic.

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Parasitofauna of the Fishes of the Falkland-Patagonian Region

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ABSTRACT

Parasitological research of fish from the Falkland-Patagonian region was carried out during the period 1972-80. As a result, the number of known parasite species [from the area] has been increased from 129 to 206 and the number of fish species studied parasitologically increased from 53 to 64. The degree of study of each group of parasites is shown. The inadequacy of research on the ciliates, myxosporidians, microsporidians, monogeneans, and parasitic copepods is noted. Some 30% of the fish species in the region have not yet been examined for parasites.

INTRODUCTION

The Falkland-Patagonian Shelf region is a part of the South American notal area and covers the shelf and continental slope of the southern extremity of South America. The region is subject to the influence of two currents: A cold Falkland Current running from the south, northward, and manifesting itself especially over the shelf, on the slope, and at great depths; and a warm, southward Brazil Current over parts of the shelf from 50 to 300 m deep. Mixing of the cold and warm waters of these currents, which occurs approximately at lat. 45°S, results in the formation of highly productive zones there.

The ichthyofauna is rather scanty on the shelf in terms of species composition. According to Hart (1946), the shelf is usually inhabited by 95 fish species. The northern part, with warmer water, produces a subtropical fauna similar to that in the Mediterranean, while the southern waters are dominated by representatives of cold-loving fauna—notothenoids, gadoids, etc. Due to the proximity of the shelf to Atlantic waters, many fish species there are common to those occurring in the Antarctic region.

With regard to the above-mentioned faunistic, ecological, and hydrographical pecularities of the Falkland-Patagonian region, as well as to the poor knowledge of the fish parasitofauna there, we conducted parasitological studies of the most abundant fish species of the region in 1972-75.

This study increased the number of fish species examined for all parasites from 53 to 64, and the number of parasite species reported from these fishes was 206 compared with the previous record of 129.

Since no analytical report on the extent of parasitism on the fishes of the Falkland-Patagonian region has been available until now, an attempt will be made in this presentation to analyze the parasitofauna of the fish of the region under study based on personal and literary data.

First of all, the absence of any evidence of the availability [presence] of the protozoan parasites such as haemogregarines and trypanosomes should be noted. Coccidia were represented by a single species, *Eimeria clupearum*, reported from the mackerel, *Scomber colias* (Evdokimova 1973). This species is a commonly reported coccidian from clupeoids of the Atlantic and Pacific Oceans.

Thirty-one species of 14 genera of Myxosporidia were found. Five species (*Zschokkella meglitschi*, *Z. globulosa*, *Davisia newfoundlandia*, *Parvicapsula asymmetrica*, and *Auerbachia pulchra*) were new locality records, and nine representatives of the genera *Zschokkella*, *Myxoproteus*, *Myxidium*, *Sphaeromyxa*, *Ceratomyxa*, and *Kudoa* turned out to be new to science. Our discovery of so many new species (30% of the total) indicates that the study of this group of parasites in the southwestern Atlantic had been given little attention.

Based upon their distribution pattern, all Myxosporidia can be classified as follows: 1) Those associated exclusively with the Falkland-Patagonian region, and 2) those occurring in other areas of the World Ocean. The first group is rather numerous and involves 24 species, or 77% of the total number. This is partly due to the endemism of the fish harboring these parasites and to their rather limited host-specificity, and to a certain extent, to the paucity of information on oceanic Myxosporidia.

A second group, consisting of seven species, is basically associated with deepwater fishes and usually occurs with its hosts all over the region. So, *Z. meglitschi*, *Z. globulosa*, *D. newfoundlandia*, and *M. coryphaenoidium* found on the shelf have been reported from Macrouridae in many areas of the World Ocean. Regarding *Z. globulosa*, this species is likely to possess a rather high ecological valency, because it has been found in both the urinary bladders and the gallbladders of many sea fishes belonging to different taxonomic groups (i.e., Macrouridae, Cottidae, Tetraodontidae, and Heteropneustidae) (Kovaliova and Gaevskaya in litt.). *Auerbachia pulchra*, described from Macrouridae of the North Atlantic and California waters, was also reported from the shelf.

The presence of *P. asymmetrica* in *Macrourus holotrachys* of the southwest Atlantic is noteworthy, because the only host ever known to harbor this parasite was the lumpfish, *Cyclopterus lumpus*, in the White Sea (Schulman 1953). There has been no indication of *P. asymmetrica* infecting fish of other Atlantic regions; therefore, its migration routes to southern waters are not clear yet. This group of widely spread species probably also includes *Chloromyxum ovatum* reported from the blue shark, *Prionace glauca*, (Kuznetzova 1977) and certain other Pacific sharks (Jameson 1929, 1931).

Microsporidia were represented by a single species, *Nosema ovoideum*, found in the liver of Patagonian hake, *Merluccius hubb-*

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si (Reimer and Jessen 1974; personal data). The paucity of the species composition of the Microsporidia fauna suggests that the study of parasites of this group has not been given due attention.

The Infusoria fauna includes three species of the genus *Trichodina*, two of which were found only on the shelf. The third, *T. oviducti*, reported from four species of skates, also on the shelf (Evdokimova et al. 1969), was first described from Barents Sea skates (Polianski 1955).

Trematoda [Digenea] is the most numerous group of parasites of fish of the Falkland-Patagonian region, numbering 50 species of 96 genera of 16 families. The families *Hemiuridae*, *Derogenidae*, *Lepocreadiidae*, and *Fellodistomidae* have the highest variety [largest number] of species. The life cycle of trematodes of the first two families is closely related to that of planktophagic fishes, which show a rather large extent of invasion [infection] (about 50 species per fish). Lepocreadiids and fellodistomids generally use benthic invertebrates as second intermediate hosts and infect fishes inhabiting the near-bottom layer which feed on those invertebrates. The same trematode species can be found in fish belonging to different taxonomic groups, but using similar items of diet. For example, *Elytrophalloides oatesi* (family Hemiuridae) were present in Macrouridae, Gadoidae, *Notothenia*, Gobiidae, etc.

The availability of numerous endemic forms (30% of the total number of species) is a characteristic feature of the trematode fauna of the region, which is evidently related to the distribution of the first intermediate hosts, the mollusks, which have a limited host-specificity for trematodes.

Additionally, the hydrographical peculiarities of the shelf may prevent the settling of the host mollusks in new oceanic areas.

The species composition of the trematode [digeneid] fauna includes *Stephanostomum lineatum*, *Lepocreadium trullaforme*, *Brachyphallus parvus*, *Dissosaccus gravidus*, and *Aponurus laguncula* occurring in the coastal Atlantic waters off of Europe and North America, and such species as *Monascus filiformis*, *Opechona orientalis*, *Ectenurus virgula*, *Derogenes varicus*, *Gonocerca* spp., and *Otodistomum* spp. are widely distributed in many areas of the World Ocean.

The explanation for the presence of elements of Antarctic origin on the shelf appears to be based on the proximity of the shelf and the Antarctic. These are: *Elytrophalloides oatesi*, *Lecithaster australis*, *Lepidapedon antarcticus*, and *Opechona magnatestis*.

It is highly possible that more extensive penetration of the Antarctic species onto the shelf is prevented by the regions [distance and hydrographic features] separating the shelf and the Antarctic.

The trematode [digeneid] fauna of deepwater macrourids, *M. holotrachys* and *Coelorhynchus fasciatus*, and the "deepwater dory," *Allocyttus verrucosus*, studied in 1975, is very peculiar. The trematode species compositon on these fishes appears to be entirely different from that on other fishes of the shelf and simultaneously very similar to the trematode fauna of some bathyal fishes of the West African continental slope.

Only two species of aspidogastrids, *Lobatostoma ringens* and *Taeniocotyle elegans*, were reported respectively from *Oncopterus darvini* from the northern part of the shelf (Szidat 1961) and from the chimaera (Kuznetzova 1974). The first species is characteristic of the subtropical and tropical waters of the western Atlantic, and the second occurs along both coasts of the Atlantic.

Monogenean trematodes [Class Monogenea] amount to 26 species of 2 genera. Of those, 12 species parasitize Chondrichthyes fishes, of which 9 species were recorded only in the southwest Atlantic. Teleosts of the shelf yielded 14 monogenean trematodes from 10 families. Some of them, *Grubea cochlear*, *Anthocotyle merluccii*, *Heterobothrium affinis*, *Kuhnia scombri*, and *Diclidophora minor*, are very common in Atlantic waters and their area of distribution is closely associated with that of their hosts. So, *G. cochlear* and *K. scombri* have been reported only from the northern shelf, where their hosts (mackerels) occur, and *A. merluccii* and *D. minor* migrate considerably further to the south with their hosts—hakes and poutassou.

At present, *Neogrubea soni*, *Tribuliforus salilotae*, and *Megalocotyloides patagonicus* are recorded only on the shelf and, evidently, are endemic species (Gaevskaya and Kovaliova 1975).

Pseudobenedenia nothothenia and *Neopavlovskioides georgianus* are two species of the Antarctic fauna that have reached as far as the shelf. The banks of the South Antilles Ridge is the most likely path of migration of such species as toothfish, *Dissostichus eleginoides*, which are the host of the above parasites. Toothfish are caught at depths to 200 m, and the depths of the banks vary between 300 and 1,200 m. Although the shelf is separated from the subantarctic zone of the Atlantic Ocean by considerable depths and the powerful Antarctic Current, the Antarctic Countercurrent, passing at great depths and overlapping the southern extremity of the Falkland-Patagonian shelf, may promote the migration of deepwater fishes to a certain extent. This might have been one of the routes taken by *Macruricotyle claviceps* to appear in this region from the Indian Ocean (Gaevskaya and Kovaliova 1977).

Fishes of the southwest Atlantic harbor few hyrocotilids, only three species having been reported from a number of Chondrichthyes fishes at different times (Kuznetzova 1974; MacDonagh 1927; Mendivil-Herrera 1946). Usually, these parasites are not strictly associated with a certain locality but occur all over the distribution area of their hosts.

Cestodes form one of the most numerous groups of parasites of Falkland-Patagonian shelf fishes—32 species of 22 genera. The overwhelming majority of mature forms, 17 species, was found in Chondrichthyes fishes with just 4 species in teleosts. The latter also yielded seven more larval cestodes whose mature stages have not yet been observed on the shelf although developing in cartilaginous fishes.

The predominance of cestodes in cartilaginous fishes is not casual [or accidental] considering the phylogenetic correlation existing between the development of this class of parasites and that of Chondrichthyes. A long-standing "parasite-host" system with these helminths has resulted in their rather limited host-specificity, which explains the great variety of the species composition of the cestode fauna of cartilaginous fishes to a certain extent. This factor is also responsible for the relative homogeneity of the cestode distribution among the cartilaginous fishes of the World Ocean. *Anthobothrium cornucopia*, for example, has been reported from sharks of the southwest, northwest, and northeast Atlantic, and *Platybothrium auriculatum* from sharks of the Atlantic and Pacific coasts of South America, etc.

There is an immediate dependence of the species composition of the cestode fauna in some species of cartilaginous fishes and their feeding patterns: The wider the spectrum of the fish feeding, the higher the variety of species composition of their cestode fauna; and, the higher the feeding rate the higher the invasion intensity [intensity of infection] (Kuznetsova 1975).

Infestation of teleosts with larval cestodes of Chondrichthyes shows wide fluctuations, which most likely depend on the place occupied by these fish in the life cycles of their parasites. Consequently, according to our data, larval *Grillotia erinaceus* were reported from 5.1% of poutassou, *Micromesistius australis*, (at an

invasion intensity of 2 to 42 parasites per fish), 15% of toothfish (1 to 12 parasites per fish), 6% of hakes (1 to 2 parasites per fish), etc.

Out of seven acanthocephalan species recorded in the southwest Atlantic, five species infecting the fish were at mature and two at larval stages. *Echinorhynchus gadi* (in six out of nine *Salilota australis* dissected) and *Corynosoma humanni* in *Notothenia ramsai* (in 11.5% of the fish) were found in this area for the first time. The first parasite is very common in Atlantic and Pacific Oceans, and the second occurs in antarctic and subantarctic waters. Two acanthocephalan species, *Aspersentis johni* and *Hypoechinorhynchus magellanicus*, are endemics in these regions.

The nematode fauna was represented by 15 species of 11 genera, *Ascarophis nototheniae* and *Contracaecum osculatum* being reported from the shelf for the first time. The first species is characteristic of antarctic and subantarctic waters (Johnston and Mawson 1945; Gaevskaya and Kovaliova 1975) and the larvae of the second species were found in the fishes of the White, Barents, Norwegian, and North Seas (Walter 1979). When describing larval *Contracaecum* from antarctic and subantarctic fishes the investigators (Johnston and Mawson 1945; Kagei and Watanuki 1975; Leiper and Atkinson 1915) noted a quite definite similarity between some of these larvae and *C. osculatum*. Careful comparison between morphometric characters of the larvae found by the authors and larval *C. osculatum* (Walter 1979) indicated a complete identity. We found these nematodes in poutassou (12% of fish), hakes (7.8%), macrourids, *M. holotrachys* (1.7%), and toothfish (2.7%).

Among nematodes reported from the southwest Atlantic, 12 species—or 80% of the total number—are characterized by a wide geographical distribution and occur in many regions of the World Ocean. This circumstance, however, is also indicative of a poor knowledge of the nematode fauna of the given region.

In the available literature we have not found any data concerning the leeches infecting Falkland-Patagonian fishes. The only leech, found on a toothfish, was considered to be a representative of the genus *Ichthyobdella*.

Parasitic copepods are rather numerous, numbering 32 species of 19 genera. Twenty species were reported from cartilaginous fishes and 13 species from teleosts. (*Caligus elongatus* was present in both types of hosts.) Most copepods are not strictly specific to their hosts, their dispersion being exclusively stipulated [controlled] by ecological factors. However, the range of some species such as *Trifur tortuosus* and *Chondracanthus palpifer* is limited to the region of distribution of their hosts, and they do not occur in other areas nor on other hosts. The data on the presence of the above-mentioned copepods on the Chilean hake, *M. gayi*, (Brian 1944) in the Buenos Aires region are incorrect. The mistake was most likely introduced during identification of the host. It is known that *M. gayi* does not occur in that region (Hart 1946). Evidence of the occurrence of parasitic crustaceans, *Brachiella lageniformis*, *Ch. palpifer*, and *Ch. merluccii* in hakes (*M. hubbsi*) of the southwest Atlantic was used to study the evolution of this species (Gaevskaya et al. 1980).

Parasitic isopods of southwest Atlantic fish are few—three *Nerocila* and one *Aega* species (Szidat 1955, 1961; Trilles 1975).

SUMMARY

As a result of the study conducted by the authors of this paper, a total of 206 species of parasites were harvested [collected] from Falkland-Patagonian fish, which exceeds the number of species known at the beginning of the study by 40%. It has become clear that the representatives of many parasitic groups, in particular Infusoria, Microsporidia, Myxosporidia, Monogenea, and Copepoda, require much more careful investigation. Besides, over 30% of the fish [residing in the area] have never been analyzed for parasitological infestation, and over 20% of the fish have been studied only poorly. Therefore, it can be suggested that as a result of further parasitological studies of the fish of this region, the number of parasite species will increase to 350-400. For comparison, it can be mentioned that fishes of the northwest Atlantic have yielded over 600 species of parasites.

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Parasitofauna of Fishes of the Whale Ridge

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ABSTRACT

Forty-six species of parasites were found in 13 fish species from the Whale Ridge area. The myxosporidian fauna was represented by 13 species of 6 genera found in 6 fish species. Monogeneans numbered four species of four genera in three fish species. The cestode fauna was represented by larval *Gymnorhynchus gigas*. The trematode [digeneid] fauna numbered eight species of six genera and was reported from eight host species. Nematodes of eight species of six genera were reported from eight fish species. Two genera of acanthocephalans were found in three host species. The parasitic copepod fauna was represented by six species of four genera found in three fish species.

Four hundred and sixty-seven specimens of 13 species of fish were examined for parasite infection from 1976 to 1978 in the Whale Ridge area. Simultaneously, the method of incomplete parasitological dissection was used to examine 768 specimens of 6 species of fish. In all, 46 parasite species were recorded.

Myxosporidia were represented by 13 species of 6 genera (*Coccomyxa*, *Ceratomyxa*, *Alataspora*, *Parvicapsula*, *Myxidium*, and *Sphaeromyxa*) found in 6 fish species. The majority of species turned out to be new to science, which indicates that the knowledge of these parasites from southern latitudes is poor. The genus *Ceratomyxa* is notable for a wide specific variety (5 species), the representatives of which are generally large forms, 0.5 mm thick (Gaevskaya and Kovaliova 1980). Myxosporidia of other genera are characterized by small sizes, nevertheless, all are well-adapted to parasitism in bathypelagic fish species.

Most Myxosporidia species (five) were recorded in *Beryx* with a certain regularity in their distribution over the ridge. Therefore, it is suggested that these parasites be used as "tags" in the study of *Beryx* populations (Kovaliova and Gaevskaya 1980).

Monogeneans were represented by four species of four genera (*Neodiplectanotrema*, *Winkenthughesia*, *Microcotyle*, and *Protomicrocotyle*) and recorded in three fish species with rather high indices of infection. For example, the infection of frostfish with *W. australis* is as high as 93%. The absence of *W. australis* from the Namibian Shelf can be noted, which along with other evidence indicates that there is no correlation [contact] between the frostfish in these two areas.

The absence of mature cestode forms from the fish examined is typical of the cestode fauna of the area. However, larval cestodes (*Gymnorhynchus gigas*) were reported from the muscles of frostfish and boarfish, and frostfish over 100 cm in length practically cannot be used for food.

The trematode [Digenea] fauna numbers eight species of eight genera recovered from six fish species. Some of the trematodes discovered (i.e., *Paraccacladium* sp., *Lampritrema mieschери*, and *Monilicaecum* sp.) use these fish as additional hosts, and others (representatives of the genera *Opechona*, *Lepidapedon*, *Podocotyle*, and *Lecithophyllum*) as final hosts. The species composition of the trematode fauna is especially wide in large fish (i.e., four species) which, perhaps, can be related to a rich food spectrum of the latter.

Eight species of nematodes of six genera (*Ascarophis*, *Spinitectus*, *Piscillania*, *Cucullanus*, *Contracaecum*, and *Anisakis*) were reported from eight fish species. In terms of frequency of occurrence, larval nematodes of the genus *Anisakis*, represented by three different types, predominated.

The acanthocephalan fauna was very poor (two species of the genera *Bolbosoma* and *Rhadinorhynchus*) were reported from three fish species at a low infection level only.

Parasitic copepods were also recorded in three fish species and were represented by six species of four genera: *Sarcotaces*, *Periplexis*, *Lophoura*, and *Brachiella*. Noteworthy is the infestation [infection] of the muscles of macrourids by large crustaceans, *Sarcotaces*, of 3 cm in length, resulting in specific swellings of the fish's body surface.

Undoubtedly, the results we obtained are preliminary and indicate that further parasitological studies are needed in this area.

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Parasitic Fauna of the Fishes of the Atlantic Part of the Antarctic (South Georgia Island and South Shetland Isles)

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ABSTRACT

Five hundred and thirty-eight specimens of 21 fish species were examined for parasites off South Georgia Island and Elephant Island (South Shetland Islands) during the period 1972 to 1979. The parasitofauna of the fishes from these areas is compared. Twenty-two species of parasites appeared to be common. The greatest number of species of parasites (19) was reported from the toothfish, *Dissostichus eleginoides*, which is a large predator, capable of accumulating the parasites of other fishes.

During 1972 to 1975 and 1978-79, 538 specimens of 21 fish species were examined for parasites off South Georgia Island and Elephant Island of a group of South Shetland Islands situated in the Atlantic Ocean south of the Antarctic convergence line. Fifty species of parasites were found, among them 30 species off South Georgia and 34 off Elephant Island. Nine species were reported from this area for the first time.

Myxosporidia were represented by three species, two of these being new to science (*Ceratomyxa* sp. and *Neoparvicapsula* sp.[2]). *Kudoa alliaria*, usually harbored by Southern poutassou of the Falkland-Patagonian Shelf, were reported from the same host off of the South Shetland Islands. It is worth noting that the species composition of myxosporidia in the Atlantic part of the Antarctic is much more scanty than on the Shelf, the ratio being 3 to 31 species.

Trematodes [Digenea] were most numerous. A total of 14 species was found, 10 off South Georgia and 11 off Elephant Island. The families Opecoelidae and Lepocreadiidae (*Plagioporus pennelli*, *Neolebouria georgianus*, and *Lepidapedon antarcticus*) were most common. *Postmonorchis variabile* was first reported from the South Georgia area (from the yellow *Notothenia*—2.6%, 1 sp.), and *Glomericirrus macrouri* (from *Chionodraco kathleena*—1.6%, 1 sp.) and *Lepidapedon* sp. (from *Notothenia kempi*—6.6%, 10 spp.) from the Elephant Island area. It may be of interest that *Elytrophalloides oatesi*, the most commonly reported parasite from the fishes of the Falkland-Patagonian Shelf, South Georgia, and Shag Rocks (Kovaliova and Gaevskaya 1978; Zdzitowiecki 1978; and the author's personal data), as well as of King George Island (South Shetland Islands), were less numerous (Zdzitowiecki 1978) and even absent from the Elephant Island area. *Elytrophalloides oatesi*, therefore, is associated with the sub-Antarctic waters and does not penetrate far to the south beyond the Antarctic convergence line.

Unlike trematodes [digeneans], monogeneans have a less representative variety of species (4), which, evidently, can be related to all parasites with a direct life cycle recovered from the fishes of this region. *Neopavlovskioides georgianus*, reported from the South Georgia area from the Patagonian toothfish (Kovaliova and Gaevskaya 1977), was found in the Antarctic toothfish off the South Shetland Islands. *Pseudobenedenoides antarcticus*, recovered from *Notothenia kempi* in the South Georgia area and from the large-eyed *Notothenia* off Berwood Bank, evidently does not penetrate into more southern latitudes. The notothenias of both South Georgia and the South Shetland Islands were equally infected with *Pseudobenedenia nototheniae*. *Diclidophora minor*, which is widely distributed among the fishes of the genus *Micromesistius* of the Atlantic, was recovered from southern poutassou off Elephant Island.

The cestode fauna numbered seven species, without any trace of adult forms. Larval *Phyllobothrium* sp., *Lacistorhynchus tenuis*, and *Scolex pleuronectis*, occurring in both investigated areas, were most common. *Dyphillobothrium* sp. individuals were found exclusively in the South Shetland Islands area in the body cavity and stomach walls of seven fish species.

Eight acanthocephalan species were reported. Larval forms were represented by three species of the genus *Corynosoma*. *Corynosoma bullosum* was predominant, heavily infecting 10 fish species in all regions. *Corynosoma hamanni* and *C. singularis* were found individually. Mature *Aspersenthis megarhynchus* were reported from the marbled *Notothenia* of both the South Georgia and Elephant Island areas, as were *Echinorhynchus* sp. from South Georgian toothfish and eelcods.

Nematodes were represented by four mature and five larval forms. Among mature nematodes, *Ascarophis notothenia* and *Cucullanellus fraseri* were most common, the latter being reported from eight fish species only from the South Georgia region. Larval *Terranova decipiens* were recovered from 11 fish species all over the region, and larval *Contracaecum osculatum* from 9 fish species off Elephant Island.

The fauna of parasitic leeches numbered two species of the genus *Cryobdella* found on six fish species from South Georgia and the Elephant Island area.

Parasitic crustaceans were represented by two species of the genus *Brachiella* reported from both regions.

On the whole, the parasitic fauna of the fishes of South Georgia and the South Shetland Islands was very diverse in terms of species composition as well as zoogeographically. Comparison of

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[2]The species mentioned here have probably been described since the manuscript was submitted in October 1981. The same is true of the genus *Neoparvicapsula*, also mentioned.

the parasitic fauna showed that 22 parasite species were common for South Georgia and Elephant Island fishes. The most diverse species composition of parasites was reported from the toothfish (*D. eleginoides*—19 species), which is a large predator capable of accumulating parasites of other fishes. The degree of resemblance of the parasitic fauna (particularly of the species composition of nematodes and cestodes) was considerably higher in the fishes of the Elephant Island region than in the same hosts of the South Georgia region, which can be attributed to an increasing proportion of krill in the diet of the fishes of the former region (Tarverdieva and Pinskaya 1980).

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On the Parasitofauna of Xiphioidea of the Northwest Area of the Indian Ocean[1]

V. R. DUBINA[2]

This report contains results of the parasitological studies of 16 sailfishes, *Istiophorus americanus*, 10 black marlins, *Makaira mazara*, and 9 specimens of the swordfish, *Xiphias gladius*, caught on longlines in the area of the Amirante and Comores Islands.

Twenty-nine species of parasitic worms were found in fishes of the family Istiophoridae—13 species in the sailfishes and 16 species in black marlins. The swordfish (Xiphiidae) was infected with eight species of helminths and parasitic copepods (Tables 1, 2, 3).

Monogenetic trematodes of the subfamily Capsalinae,[3] which are specific parasites of the Scombridae, are represented in the Xiphioidea by such genera as *Capsala* Bosc, 1811; *Tristomella* Price, 1960; *Capsaloides* (Verill, 1875) Price, 1938; and *Tristoma* Couvier, 1817. *Capsala ovalis* and representatives of the genus *Capsaloides* live parasitically only in marlins. Capsalidae of the genus *Tristoma* live in the gills of swordfish. Species of the genus *Tristomotella* are found in the sailfishes and marlins. *Tristoma coccineum* generally parasitizes the gills of young specimens of the swordfish.

The tapeworm, *Bothriocephalus manubriformis*, infects both sailfishes and marlins. *Fistulicola plicata* was found only in the swordfishes. Larvae of the cestode *Trypanorhyncha* gen. sp. infect all representatives of the Xiphioidea. The bothriocephalids were found in large numbers in the intestines and may obstruct the intestinal passages of both sailfishes and marlins. As I observed, *Fistulicola plicata* specimens may sometimes perforate the intestinal walls of swordfish and enter their abdominal cavities.

The trematodes [digeneids] detected in sailfishes and marlins belong to the families Hirudinellidae (one species) and Didymozoidae (four species), both fish species being infected by *Metadidymozoon branchiale*.

Nematodes are represented by the species *Contracaecum histiophorus* and *C. incurvum*, typical of Xiphioidea.

The parasitic copepods found in the Scombridae belong to the families Lernaeidae and Caligidae. But if *Gloipotes huttoni* is a specific copepod living on the skin of Xiphioidea, then *Penella orthagorici* also occurs in other Scombridae.

Thus, the Xiphioidea fishes I studied show a strongly marked specificity of the monogeneid helminthofauna for each host. At the same time, a similarity is found in the composition of larvae of Cestoda, didymozoids, and parasitic copepods, which may be accounted for by the similar ecology, pelagic habitat, common food items, and close phylogeny of these fishes.

[1]No Literature Cited section was supplied by the author.

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[3]The systematics of this subfamily is given according to Price (1960).

Table 1.—Parasitofauna of the sailfish, *Istiophorus americanus*.

Species	Number of fish dissected	Number of fish infected	Location	Intensity of infection
Tristomella pricei (Hidalgo, 1959) Price, 1960 (=*Capsala pricei*)	10	3	Snout, skin of the mouth	1-4
Tristomella sp.	10	10	Skin, furrow of the fin	5-27
Tristomella sp.	10	7	Skin, furrow of the fin	3-5
Hirudinella fusca (Bosc, 1802)	10	2	Stomach	1-3
Metadidymozoon branhiale Yamaguti, 1970	10	2	Gill plates	18-94
Unitubulotestis istiophorus sp.	10	1	Abdomen	3
Neodidymozoon midistoma sp.	10	2	Operculum	2-4
Contracaecum histiophorus Yamaguti, 1935	10	1	Stomach	6
Bothriocephalus manubriformis Linton, 1889	10	10	Pyloric caeca, intestines	> 100
Tentacularia sp. larvae	10	2	Intestines, stomach	5-8
Trypanorhyncha gen. sp. larvae	10	8	Intestines, stomach	12-37
Gloipotes huttoni Thomson, 1889	10	10	Skin, tail, fins	3-28
Penella orthagorici Wright, 1870	10	2	Skin	1

Table 2.—Parasitofauna of the black marlin, *Makaira mazara*.

Species	Number of fish dissected	Number of fish infected	Location	Intensity of infection
Capsala ovalis (Goto, 1894) Yamaguti, 1968	16	16	Gill arches	2-54
Tristomella pricei (Hidalgo, 1959) Price, 1960 (=*Capsala pricei*)	16	2	Snout, skin of mouth	1-2
Tristomella sp.	16	3	Skin	1-14
Capsaloides nairagi Yamaguti, 1968	16	2	Gill arches	1-2
Capsaloides sp.	16	6	Gills, between gill arches	11-137
Hirudinella fusca (Bosc, 1802)	16	4	Stomach	1-3
Unitubulotestis makairi Nikolaeva and Dubina, 1978	16	3	Body cavity	2
Wedlia submaxillaris (Yamaguti, 1970) Nikolaeva, 1978	16	2	Gill filament	4-8
Neodidymozoon macrostoma Yamaguti, 1970	16	3	Dorsal fin, gill arches	4-6
Metadidymozoon branhiale Yamaguti, 1970	16	3	Gill plates	12-23
Contracaecum incurvum (Rud., 1819) Baylis and Daubney, 1922	16	10	Stomach, intestine	2-97
Contracaecum sp. larvae	16	12	Serose coverings of the internals	1-24
Bothriocephalus manubriformis Linton, 1889	16	12	Intestine	14->100
Trypanorhyncha gen. sp. larvae	16	7	Serose of body cavity	12-29
Gliopotes huttoni Thomson, 1889	16	14	Skin	14-76
Penella orthagorici Wright, 1870	16	1	Skin	2

Table 3.—Parasitofauna of the swordfish, *Xiphias gladius*.

Species	Number of fish dissected	Number of fish infected	Location	Degree of infection
Tristoma coccineum Cuvier, 1817	9	2	Gills	8-34
Tristoma adintegrum Yamaguti, 1963	9	3	Gills	1-2
Fistulicola plicata Rudolfi, 1819	9	9	Intestine	14-32
Nybelinia sp. larvae	9	5	Stomach	3-11
Trypanorhyncha gen. sp. larvae	9	9	Stomach, intestine	7-35
Contracaecum incurvum (Rud., 1819) Baylis and Daubney, 1922	9	1	Stomach	12
Gloipotes huttoni Thomson, 1889	9	6	Skin	3-15
Penella orthagorici Wright, 1870	9	2	Skin	1

Parasites as Indicators of Specific Features of Fish Ecology

S. M. KONOVALOV[1] and T. E. BUTORINA[2]

ABSTRACT

An analysis of the results of a number of investigations involving the use of parasite-indicators in studies of fish ecology was conducted. Using salmon species as an example we concluded that this approach is very promising, not only for comparisons of ecology of closely related species, but also of interspecific forms and for studies of the biology of populations (isolates) and subpopulations (subisolates), as well as of groups being formed within subisolates.

Use of parasites to study the ecology of their hosts (fish) has a rather long history. Use of this method is possible only in cases where the life history of a parasite is well studied and the approximate circle of its intermediate hosts or place of infection (for parasites with direct cycles of development) is known. Even the first works of the Soviet parasitology school under V. A. Dogiel accomplished on sturgeons (Dogiel and Bykhovski 1939) and then on other marine and freshwater fishes (Shulman et al. 1959) showed the possibilities of such an approach to studies of host ecology. As a result of using parasitological data and by tagging, Margolis and his colleagues managed (Margolis et al. 1966) to explain the marine distribution and migration of sockeye salmon of the Asian and American stocks at the level of Bristol (all the isolates are of the Bering Sea coast of Alaska) and Kamchatka isolate complexes (all the isolates are of Kamchatka Peninsula) (Figs. 1, 2). Investigations made by English and Canadian parasitologists (Kabata 1963; Margolis 1965; Margolis et al. 1966) which disclosed fundamental solutions were employed by ichthyologists for practical conclusions.

The studies made by the authors indicated above on anadromous salmons provided significant data on the marine and freshwater periods of their lives. As did the previously mentioned scientists, S. M. Konovalov used parasites as indicators of local sockeye salmon stocks in 1971. It was found that by employing not only the qualitative features (i.e., selected parasite species) but also the quantitative ones (extensiveness and intensiveness of invasion), we were able to differentiate not only the complexes of isolates but some local stocks (isolates). In particular, we managed to identify fish from Kurilskoye Lake (Kamchatka), but only at the first year of life, before they began mixing with American stocks, and during their spawning migration. Combined with special features of scale structure, [these techniques] permitted us to study the entire marine period of life of the local stock and to understand the rules of distribution of the fish of Asian and American origin as well as of the different stocks in the high seas during feeding and wintering. It was revealed that local sockeye stocks, which are highly isolated during spawning, became mixed with each other during the feeding and wintering periods of their marine [high seas] phase of life. S. M. Konovalov in cooperation with I. B. Birman discovered the feeding and wintering sites as well as the feeding, wintering, and spawning migrations of different age groups of Kurilskoye Lake sockeye salmon (Fig. 3).

A number of proposals of practical importance for the regulation [management] of sockeye fishing in the North Pacific was made on the basis of these studies. Moreover, these works served to encourage studies of the sea [oceanic] period of other salmon [species] using ichthyological data as a basis. To date, much infor-

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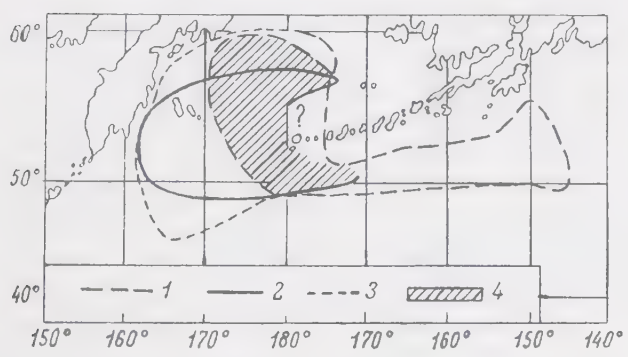

Figure 1.—Distribution of immature Alaskan and Kamchatka sockeye salmon in the North Pacific (according to Margolis et al. 1966). 1 = boundary of the areas of western Alaska sockeye; 2 = boundary of the areas of Kamchatka sockeye; 3 = supposed boundary of the areas of Kamchatka sockeye; 4 = mixed areas.

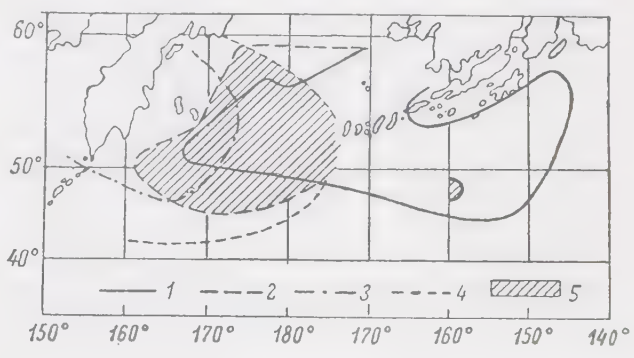

Figure 2.—Distribution of mature Alaskan and Kamchatka sockeye salmon in the North Pacific (according to Margolis et al. 1966). 1 = boundary of the areas of western Alaska sockeye; 2 = supposed boundary of the areas of western Alaska sockeye; 3 = boundary of the areas of Kamchatka sockeye; 4 = supposed boundary of the areas of Kamchatka sockeye; 5 = mixed areas.

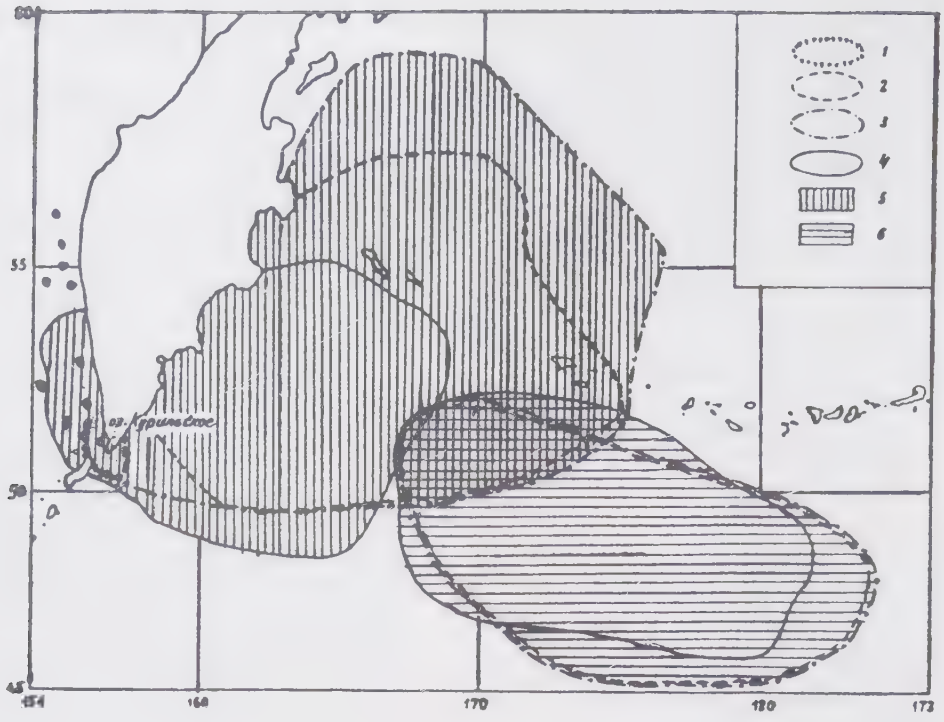

Figure 3.—Distribution of various age groups of sockeye salmon of Lake Kurilskoye in the northern part of the Pacific Ocean. 1 = distribution of juveniles in the autumn of the year of their downstream migration; 2 = distribution of sockeye following their first winter in the ocean; 3 = following their second winter in the ocean; 4 = following their third winter in the ocean; 5 = distribution of sockeye in the autumn; 6 = in the spring.

mation on the biology of the sea [oceanic] phase of many Pacific salmons has been obtained.

Analysis of the species composition of parasites enables one to determine the preferred food organisms (pelagic, benthic, etc.) used by the fish species and forms under investigation. This is especially important because the rapid digestion of food by fish as well as by other animals causes great difficulties in making judgements of dietary types and preferences [from analysis of stomach contents]. Thus, the idea of sockeye as the exceptional planktophage (Foerster 1968) was clarified and supplemented as a result of parasitological analyses of sockeye juveniles (Konovalov 1971). It was found that besides plankton, the diet of sockeye may consist of flying insects which fall into the water and their larvae, as well as bottom invertebrates.

Also, we used the parasites to clearly distinguish the char belonging to the various ecological groups of Lake Azabachye (Kamchatka). Thus, the cestodes *Diphyllobothrium* sp. and *Eubothrium salvelini* infect predaceous char and are absent on the benthophagic [benthos feeders] ones (malma). We can distinguish between not only freshwater predators and benthophages with the aid of *Diphyllobothrium* sp., but also the anadromous ones because the char retains its parasites during the time it is at sea as well. On the other hand, *Cyathocephalus truncatus* may be observed on mature benthophagic fish but is absent on predatory char of the same size. This verifies the different feeding habits of these fishes.

Very often it is difficult to distinguish the freshwater and anadromous forms of char (of the genus *Salvelinus*), coho, *Oncorhynchus kisutch*, and sockeye, *O. nerka*. By examining the parasitofauna of fish we may in many cases, using only one specimen, decide whether the fish has been to sea or not. Larval *Pelichnibothrium speciosum*; the thorny-headed worms, *Echinorhynchus gadi* and *Bolbosoma caenoforme*; and the estuarine [cestode] *Eubothrium crassum* can be found only on those fish which have migrated to the sea or estuary and serve as indicators of anadromous forms. This is especially important in cases in which anadromous forms reside in freshwater over a long period of time and do not differ in appearance (practically) from the river forms, as may be observed with char.

Parasitological analysis allowed us to distinguish wintering anadromous, predaceous char in Lake Azabachye. Anadromous and freshwater kundzha, *Salvelinus kundzha*, have different species of the cestode genus *Eubothrium*. Anadromous ones have *E. crassum* while those confined to the river have *E. salvelini*. We did not observe [find] both Cestoda species on these fishes simultaneously. Moreover, it was found that anadromous forms differ, as a rule, from freshwater ones by weaker infections of the freshwater parasites typical for these fishes.

During growth and development most fish species change from one diet type to another at ontogenesis. We managed to catch such a moment in char juveniles in Lake Azabachye only with help of parasite-indicators. Investigations of the age dynamics of their parasitofauna, conducted by the authors, disclosed that a difference between lacustrine and brook chars occurs even during their first year, from an ecological point of view. Differentiation of lacustrine juveniles into predators and benthophages takes place during the second year of life (when the char attain body lengths of 10 cm and more).

Parasitological data provide not only qualitative characteristics of the composition of the food of fish but there have been some efforts to use parasites in the quantitative assessment of fish feeding (Kennedy 1969; Kuperman 1975). Thus, on the basis of the data on contamination [by parasites], B. I. Kuperman determined the number of ruffes eaten by burbot in the Rybinskoye reservoir during its feeding. The magnitude of the figures obtained

by him proved to be very close to the data secured by ichthyologists for the same period.

During the last decade we collected vast material which disclosed that parasites might be used to study the ecology of elementary populations (subisolates). Analyzing the levels of infection by *Diphyllobothrium* sp. of juvenile and spawning age sockeye in Lake Azabachye, we managed to learn that fish with different scale types, as well as of different sex but with a similar scale pattern, have different levels of infection of this parasite. Mature tapeworms of *Diphyllobothrium* sp. used for the model were found in bears, dogs, gulls, and terns in Lake Azabachye (Butorina and Kuperman 1981). The first intermediate host of these cestodes are copepods of the species *Cyclops scutifer* (Kuperman 1978). Sockeye salmon are parasitized by plerocercoids, which are concentrated on the external side [peritoneal side] of the stomach and never die away [disappear] when the fish passes from freshwater into saltwater and back even though the life span of fish at sea reaches 4 yr.

Examination of samples of about 25 individuals of each separate subisolate every year revealed the existence of a complicated trophic structure of sockeye subisolates. It was found that juveniles of one [each] year-class of every subisolate may be subdivided into groups which differ in preference for copepod consumption. We also uncovered different intensities and extensities [prevalences] of invasion [infection] of mature fish by *Diphyllobothrium* sp. We distinguished conventional planktophages (whose preferable diet is copepods) and benthophages (whose preferable diet is flying insects and benthic organisms). Also, if juveniles remain in freshwater for a second year, four groups will appear, planktophage (1st year) × planktophage (2nd year); planktophage (1st year) × benthophage (2nd year); benthophage (1st year) × planktophage (2nd year); and benthophage (1st year) × benthophage (2nd year). Hence, sockeye juveniles migrate from Lake Azabachye at the ages of 1 and 2 yr and have six trophic strata and the same number of groups in every subisolate.

Comparison of the mean intensity of invasion [infection] of sockeye groupings by *Diphyllobothrium* sp. with one or another scale type in different subisolates over many years revealed rather obvious differences in both spring and summer races. Males or females of one subisolate differ by several times from males or females of the other in mean infection levels. Thus, the relation of mean intensities of infection of males with the scale of "b" type of subisolates 16 and 6 comprised 4.6 times in 1975. The same parameter [measurement or comparison] for males with "b"[3] scale type for subisolates 13 and 2 was 2.6 times. This relation for subisolates 4 and 6 with the males with scale of "bb" type was 2.9 in 1975. In 1970, females with the same scale type showed a difference between the mean subisolate intensities of 24 and 27, 2.7 times [that in 1975]. The difference in the quantity of plankton consumed for the same freshwater period comprised from 2 to 7 times. Thus, there are fish groups with a different growth rate within the subisolate. This is affirmed by the peculiarities of scale structure, which are well known for expressing selectivity of the food available to the sockeye while it is in freshwater.

Simultaneously, over 11 yr we collected a large amount of data on the invasion by *Diphyllobothrium* sp. of fish of one generation of the same subisolate of similar freshwater age and scale type, but of different sex. It was found that in most cases (95% or more) there were significant differences between males and females in extensity [prevalence] and intensity of invasion [infection] by this parasite, as it was observed with trophic groupings. Males, as a rule, were characterized by a higher level of infection and, hence, by more active consumption of copepods [or vice versa]. Females were notable for their mixed diet. The relation of mean intensity of invasion of males to the corresponding female index was dominant, i.e., 1.5, with the maximum figure being up to 13.9 times higher (Fig. 4A). Thus, we distinguished another trophic level within a subisolate. Each subisolate may total [contain] up to 12 trophic groups simultaneously, six for males and six for females (Fig. 4).

In 1974, S. M. Konovalov conducted investigations of sockeye salmon which were heavily infected by *Diphyllobothrium* sp. in Lake Iliamna (Alaska) (Fig. 4B). In six of seven cases, males had a higher intensity of invasion (two or more times) than females. Therefore, we may conclude that trophic divergence of sockeye salmon may be observed [may occur] everywhere, since they are found within isolates of both American and Asian continents. This phenomenon is also observed in other Pacific salmons. Thus, we found trophic groups of feeding juvenile silver salmon in Lake

[3]Original manuscript used "h" scale type here. It appeared to have been struck over until it looked like a "b." Since it is totally out of "sync" with the rest of the manuscript, it has been replaced with a "b."

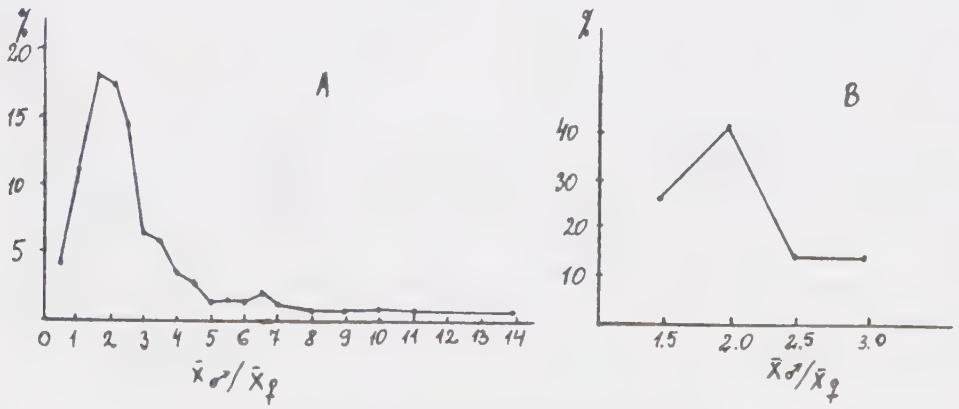

Figure 4.—Distribution of sockeye spawners of the same age- and scale-type from the different subisolates by level of differences in invasion by parasite-indicator *Diphyllobothrium* sp. pl. depending upon the sex. A - Azabachye Lake (number of studied cases is 284); B - Iliamna Lake (number of studied cases is 7). Note: relation $\bar{X}\sigma$ / $\bar{X}\varphi$ shows the level of invasion of males relating to females.

Azabachye which prefer insects, benthos, or fish fry in their diet and, consequently, had different levels of parasite infection (Konovalov 1974; Butorina and Kuperman 1981).

An interesting investigation of the biology of kokanee of Lake Kronotskoye (Kamchatka) was accomplished by S. I. Kurenkov (1979). Because of strong waterfalls this lake is isolated from the spawning migrations of anadromous sockeye and other Pacific salmons and is inhabited by freshwater sockeye which spend their entire lives within the lake. Studies of the parasitofauna of kokanee from different spawning grounds (i.e., of different subisolates) helped to reveal the existence of two trophic forms: Benthophages and planktophages (Fig. 5). However, in Azabachye Lake and Iliamna Lake anadromous sockeye form trophic groups within subisolates, and in Lake Kronotskoye formation of these groups is observed at the subisolate level. In other words, S. I. Kurenkov distinguished a great number of subisolates in which planktonic organisms were the preferred diet of all the individuals, as well as the subisolates—consisting of those fish preferring to feed on benthic organisms and flying insects (Kurenkov 1979). Parasites are such sensitive indicators of the feeding habits of the groups of individuals within elementary populations that now there are no other [or no more] reliable methods of recording the level of consumption of any type of diet for a long period. This is why the use of parasite-indicators is still the only method of distinguishing trophic groups.

Population biology discloses a number of interspecific adaptations which lead to a reduction of competition between the individuals of a population. For example, different growth rates cause [affect] diet by [feeding on] different-sized organisms [?].[4] The trophic adaptation discovered shows again the difficulty of population adaptation to the reduction of competition between individuals in critical periods of their life history.

Thus, analysis of the investigations of many years dealing with studies of fish ecology with the help of parasite-indicators allows us to conclude that the above approach is very promising, not only for comparison of the ecology of closely related species but also of interspecific forms and for studying the biology of populations (isolates) and subisolates (subpopulations) as well as of the groups being formed [established] within subisolates. At that, in some cases (e.g., trophic groups of anadromous forms of the genus *Salvelinus*) it is difficult to imagine other approaches and methods which would permit solution of the problems stated. On the basis of the above, we may consider it advisable to broaden [increase] the exploitation of parasitological data for the study of fish biology.

[4]This sentence is presented as it was in the original typescript. Words in brackets are the editor's effort to clarity. It is still confusing. The authors probably meant to indicate that competition for food, even within the same population of fish, was reduced or affected in that individuals which grow faster eat larger prey, leaving the smaller prey for smaller, slower growing individuals. Thus, competition for food is affected. Obviously fish with greater access to suitable food (below a threshold level) will grow faster than those which are food-deprived.

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[5]Not all citations mentioned in the text are included here. Also, some Literature Cited do not appear in the text.

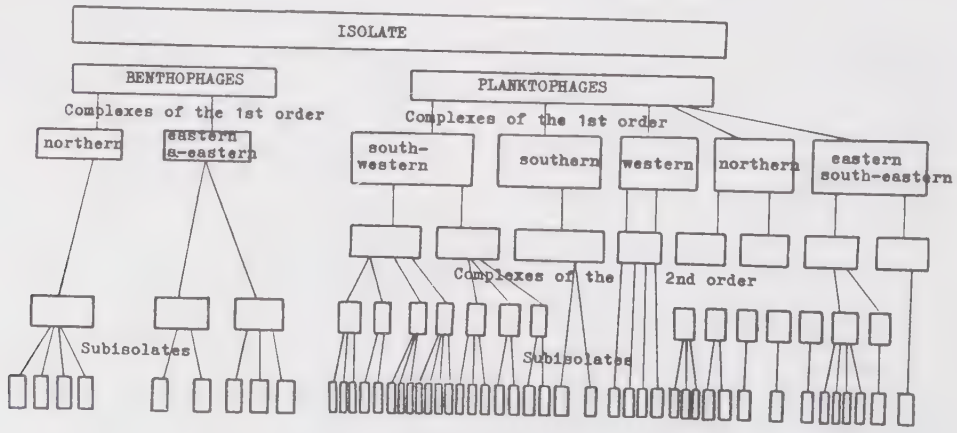

Figure 5.—Spatial structure of the kokanee population of Lake Kronotskoye.

The Taxonomic Composition and Origin of Fish Helminths in the Epipelagic Zone of the World Ocean

S. E. POZDNYAKOV[1]

The epipelagic zone is a peculiar and very interesting biotope parasitologically. At present, 738 species of helminths are registered [recorded] from about 260 to 300 fish species inhabiting open waters (Parin 1968; Cohen 1970; Nikolski 1980). The most abundant of them are trematodes [digeneids], of which 370 species (from more than 2,500 recorded sea fishes) are related to [are associated with] fish of the epipelagic zone. Trematodes of the families Hirudinellidae, Syncoeliidae, and Accacoeliidae and many subfamilies of the family Didymozoidae (i.e., Adenodidymocystinae, Colocyntotrematinae, Glomeritrematinae, Koellikeriinae, Metadidymozoinae, Neodiplotrematinae, Nephrodidymotrematinae, and Reniforminae) form [constitute] a true oceanic group. The genera of the Didymozoidae subfamilies Annulocystiinae, Didymocodiinae, Didymozoinae, Nematobothriinae, Opepherotrematinae, Ossoodidymocodiinae,[2] Phacelotrematinae, Pseudocolocyntotrematinae, Sicuotrematinae, Skrjabinozoinae, and separate [certain or different] genera of the abundant suborder Hemiurata compose a neritic-oceanic group. Trematodes of the families Bucephalidae, Allocreadiidae, Opecoelidae, Lepocreadiidae, and Fellodistomidae are not common for the pelagic zone, but are found there occasionally.

Of the more than 2,200 known species, only 139 species of monogenetic flukes [Monogenea] are found in epipelagic fish. These oceanic species belong to the genera *Capsala*, *Caballerocotyla*, *Capsaloides*, and *Tristoma* (family Capsalidae); *Erpocotyle* (family Hexobothriidae); *Hexostoma* and *Neohexostoma* (family Hexostomatidae); and *Dionchus* and *Loimosina* (family Dionchidae). Many genera of the families Monocotylidae, Gastrocotylidae, and Axinidae are far-neritic [distant neritic] and neritic ones.

One hundred and thirty-six species of Cestoda from more than 800 marine fishes occur in the epipelagic zone. Truly oceanic Cestoda are representative of a portion of the family Litobothridae, i.e., the genera *Hepatoxylon* and *Tentacularia* (order Trypanorhyncha) and *Fistulicola* (family Ancistrocephalidae), as well as a number of species of the *Nybelinia* genus (family Tentacullariidae).

Among 42 species of thorny-headed worms from fish of the oceanic epipelagic zone, none can be related to a really oceanic group. The family Rhadinorhynchidae is nerito-oceanic. Species of the other families occur occasionally in the epipelagic zone.

Only certain Nematoda species of the families Anisakidae, Philometridae, Cucullanidae, Camallanidae, and Rhabdochonidae are found in the oceanic fish, as was observed in the case of the previous group.

Analysis of the taxonomic composition of fish helminths in the epipelagic zone shows the close relationship between the oceanic helminthofauna complex and the neritic-pelagic one. Separation of the oceanic group from the neritic took place probably in the mid-Tertiary period, i.e., during the formation of the epipelagic ichthyocoenosis. There are some oceanic helminthofaunistic [helminthofaunal] groups in the epipelagic zone of the World Ocean. The most abundant among them are tropical and related subtropical groups. They form in the equatorial tropical and central water masses. The nuclei of tropical and subtropical groups are in the range of the productive waters of the North and South tropical divergences and at the periphery of the North and South subtropical and tropical convergences, as well as the area of eddy-causing geostrophic currents. Independent oceanic helminthofaunistic [helminthofaunal] groups are absent from the boreal and notal waters. Subtropical and tropical species of helminths penetrate those waters along with their hosts as the latter forage in the boreal and notal waters, and the boreal and notal species are carried to the high seas by fishes able to leave the coastal and neritic waters at times in their lives. The ocean helminthofaunistic groups are lacking in arctic and antarctic waters.

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[1]Pacific Research Institute of Fisheries and Oceanography (TINRO), Vladivostok, U.S.S.R.

[2]The spelling of this subfamily is unclear due to strike-overs in the original typescript. It could have been Osteodidymocodiinae.

Zoogeographical Characteristics of the Helminths of Fishes From the Antarctic Zone of the World Ocean[1]

V. N. LYADOV[2]

The zoogeography of parasites of sea fishes has been discussed in a considerable number of Soviet and foreign papers (Dogiel and Bykhovski 1939; Schulman and Schulman-Albova 1953; Schulman 1959; Polianski 1955; Strelkov 1956; Zhukov 1960; Lebedev 1967; Parukhin 1972, 1976; Konovalov 1971; Manter 1947, 1955; Yamaguti 1963; and others) in which the distribution of helminths is analyzed almost throughout the entire World Ocean—except for the vast areas of the subantarctic and antarctic zones. This may be accounted for by the fact that the parasite fauna of fishes of these areas is little known because sufficient data are not available in the literature on the species composition of fish parasites to permit a detailed zoogeographical analysis of parasitic worms of antarctic fishes.

The most thorough investigations of fish parasites of the antarctic zone of the World Ocean were made by Gussev (1967) who described about 20 species of fish helminths and, in general, about 50 species from all species of animals. In their work, Gaevskaya and Kovaliova (1976) point to the scarcity of the trematode fauna and provide data on nine species of trematodes found in the fishes of the families Nototheniidae, Chaenichthyidae, and Bathydraconidae

Of foreign works, those of Prudhoe and Bray (1973), in which data on the distribution of the trematode and monogenean fauna in the antarctic zone of the Atlantic Ocean are presented, should be noted. Here I employ data from my own research and from the literature in an attempt to analyze the distribution of parasitic worms in the antarctic zone and adjacent waters of the Pacific, Indian, and Atlantic Oceans, ignoring leeches and parasitic crustaceans.

The most abundant group of helminths is represented by the trematodes [digeneids]. Thirty-five species of these flatworms are registered for this region of the World Ocean (Table 1). Analysis of the trematode fauna of the Kerguelen and Glass [Glacial] subregions, which are separated by vast water areas with abyssal depths, revealed a considerable specific affinity of trematodes in these regions. Thus, from the total number of this group of parasites 13 species of trematodes [digeneids] are common to both subregions of the antarctic zone. These are *Gonocerca phycidis*, *Derogenes varicus*, *Lecithaster australis*, *Plagioporus antarcticus*, *Opechona magnatestis*, *Lepocreadium trullaforme*, *Neolepidapedon antarcticus*, *Lecithophyllum anteroporum*, *Elytrophalloides oatesi*, *Glomericirrus macrouri*, *Genolinae bowersi*, *Postmonorchis variabilis*, and *Descoveritrema markowskii*. However, in spite of the affinity of the trematode [digeneid] fauna in these regions, endemism is rather strongly marked among them. In the Kerguelen subregion seven species of trematodes [digeneids] characteristic of this area are registered [recorded]: *Gonocerca muraenolepisi*, *G. medius*,[3] *Plagioporus* sp., *Stenakron kergeulense*, *Lomosoma kergeleni*, *Benthotrema melanostigmi*, and *Steganodermatoides kergeleni*. In the Glacial subregion 11 species of trematodes [digeneids] are recorded: *Plagioporus pennelli*, *Lepidapedon* sp., *L. garrardi*, *L. antarcticus*, *Neolepidapedon trematomi*, *N. dubius*, *Lecithocladium orustatum*, *Stenakron* sp., *Otodistomum cestoides*, *Otodistomum* sp., and *Neoleburia georgiensis*. Despite the closeness of the regions of the Kerguelen subregion and South Australia, their trematode [digeneid] fauna relations were not marked. There were only two common species of trematodes: *Gonocera phycidis* and *Elytrophalloides oatesi*, while the relationships of the trematode [digeneid] fauna of the Patagonian shelf were expressed more strikingly, there were five common species: *Gonocerca phycidis*, *Derogenes varicus*, *Plagioporus antarcticus*, *Lepocreadium trullaforme*, and *Elytrophalloides oatesi*.

Comparing the helminthofauna of the Kerguelen subregion with that of the tropical Indian-West Pacific and South Moderate regions, it should be noted that, according to the data of Parukhin (1976), 6 families of trematodes [digeneids] (Monorchidae, Opecoelidae, Lecithasteridae, Hemiuridae, Halipegidae, and Lepocreadidae) of 17 families and 3 species were common for the Indian Ocean and some other regions of the World Ocean.

Of the 10 known species of monogenetic trematodes of the antarctic region of the World Ocean, *Pseudobenedenia notothenia* was common for all regions. *Pseudobenedenoides shorti*, *P. antarcticus*, *Neogrubea stromateae*, *Pavlovskioides prudhoei*, and *Neopavlovskioides georgianus* were specific species of monogeneids of the Glacial subregion, and *Neopavlovskioides dissosthychi*, *Macruricotyle clavipes*, *Rajoncocotyle* sp., and *Acanthocotyle* sp. were characteristic monogeneids for the Kerguelen subregion.

The cestode fauna of this region has been investigated only poorly. Because of this we did not find sufficient data in the Soviet and foreign literature to permit an analysis of cestode distribution in this region of the World Ocean. Thus, we can list only seven species of cestodes: *Neobothriocephalus* sp., *Bothriocephalus* sp., *Hepatoxylon* sp. larvae, *Phyllobothrium* sp., *Acanthobothrium* sp., *Scolex pleuronectis*, and *Tetraphyllidea* sp. larvae, found in the fishes of the Kerguelen subregion. Parallel with this, it should be noted that combined species of the larvae of the cestodes *Scolex pleuronectis* and *Tetraphyllidea* sp. were widely distributed, not only in antarctic waters, but also in other regions of the World Ocean.

The acanthocephalan fauna in antarctic fishes was represented by five species: *Aspersentis megarhynchus*, *Hypoechinorhynchus magellanicus*, *Echinorhynchus debenhami*, *E. campbelli*, and *Corynosoma hamanni*. Of the fauna of thorny-headed worms of the Glacial subregion, *E. campbelli* should be considered as endemic,

[1]No Literature Cited section was supplied by the author. Most citations are presented in Literature Cited sections of other papers, however.

[2]The Azov-Black Sea Research Institute of Marine Fisheries and Oceanography (AzCherNIRO), U.S.S.R.

[3]Though given as a new species in the original typescript, this species probably was first described elsewhere. It obviously is not described in this paper.

Table 1.—Distribution of parasitic worms in the Antarctic region of the World Ocean.

NN	Species of parasite	Regions:	Patagonian Shelf	Glacial Subregion	Kerguelen Subregion	South Australia
		Trematodes [Digeneans]				
1	*Gonocerca phycidis*		+	+	+	+
2	*Gonocerca muraenolepisi*		–	–	+	–
3	*Gonocerca medius*		–	–	+	–
4	*Derogenes varicus*		+	+	+	–
5	*Lecithaster australis*		–	+	+	+
6	*Plagioporus antarcticus*		+	+	+	–
7	*Plagioporus* sp.		–	–	+	–
8	*Plagioporus penelli*		+	+	–	–
9	*Opechona magnatestis*		–	+	+	–
10	*Opecoelus scorpaenidicola*		–	–	–	+
11	*Pseudopecoelus piriformis*		–	–	–	+
12	*Lepocreadium trullaforme*		+	+	+	–
13	*Lepidapedon* sp.		–	+	–	–
14	*Lepidapedon garrardi*		–	+	–	–
15	*Lepidapedon antarcticus*		–	+	–	–
16	*Neolepidapedon trematomi*		–	+	–	–
17	*Neolepidapedon antarcticus*		–	+	+	–
18	*Neolepidapedon dubius*		–	+	–	–
19	*Neolepidapedon helicoleni*		–	–	–	+
20	*Lecithocladium crustatum*		–	+	–	–
21	*Lecithophyllum anteroporum*		–	+	+	–
22	*Elytrophalloides oatesi*		+	+	+	+
23	*Glomericirrus macrouri*		–	+	+	–
24	*Genolinea bowersi*		–	+	+	–
25	*Helicometra scorpaenae*		–	–	–	+
26	*Stenakron kerguelense*		–	–	+	–
27	*Stenakron* sp.		–	+	–	–
28	*Otodistomum cestoides*		–	+	–	–
29	*Otodistomum* sp.		–	+	–	–
30	*Postmonorchis variabilis*		–	+	+	–
31	*Discoveritrema markowskii*		–	+	+	–
32	*Neoleburia georgiensis*		–	+	–	–
33	*Lomosoma kergeleni*		–	–	+	–
34	*Benthotrema melanostigmi*		–	–	+	–
35	*Steganodermatoides kergeieni*		–	–	+	–
		Monogeneans				
1	*Pseudobenedenia nototheniae*		+	+	+	+
2	*Pseudobenedenoides shorti*		–	+	–	–
3	*Pseudobenedenoides antarcticus*		–	+	–	–
4	*Neogrubea stromateae*		–	+	–	–
5	*Pavlovskioides prudhoei*		–	+	–	–
6	*Neopavlovskioides dissosthychi*		–	–	+	–
7	*Neopavlovskioides georgianus*		–	+	–	–
8	*Macruricotyle clavipes*		–	–	+	–
9	*Rajoncocotyle* sp.		–	–	+	–
10	*Acanthocotyle* sp.		–	–	+	–
		Cestodes				
1	*Neobothriocephalus* sp.		–	–	+	–
2	*Bothriocephalus* sp.		–	–	+	–
3	*Hepatoxylon* sp. larvae		–	–	+	+
4	*Phyllobothrium* sp.		–	–	+	+
5	*Acantobothrium* sp.		–	–	+	–
6	*Scolex pleuronectis*		+	+	+	+
7	*Tetraphyllidea* sp. larvae		+	+	+	+
		Acanthocephala				
1	*Aspersentis megarhinchus*		–	+	+	–
2	*Aspersentis* sp.		–	–	+	–
3	*Echinorhynchus debenhami*		–	+	+	–
4	*Echinorhynchus campbelli*		–	+	–	–
5	*Corynosoma hamanni*		+	+	+	+
		Nematodes				
1	*Ascorophis nototheniae*		+	+	+	+
2	*Cucullanellus fraseri*		–	+	+	–
3	*Contracaecum nototheniae*		–	+	+	–
4	*Anisakis* sp. larvae		+	+	+	+
5	*Contracaecum* sp. larvae		+	+	+	+
6	*Terranova* sp. larvae		+	+	+	+

while the other four species were characteristic for all antarctic regions.

The nematode fauna of fish of Antarctica was represented by six species: *Ascarophis nototheniae*, *Cucullanellus fraseri*, *Contracaecum nototheniae*, *Anisakis* sp. larvae, *Contracaecum* sp. larvae, and *Terranova* sp. larvae, which were widely distributed in waters of this region of the World Ocean and were antarctic circumpolar species.

The existence of such an important similarity of the helminthofauna of fish of the Kerguelen and Glacial subregions could be explained first of all by the origin and development of the Antarctic fish fauna. The ichthyofauna of Antarctica is interesting in its antiquity and originality, which has been determined by the presence of endemic genera and species of the group Notothenii-formis. This fish taxon, characteristic for the antarctic and subantarctic regions and almost completely limited by their boundaries, has developed a great quantity of forms which differ by structure, appearance, and mode of life. These facts allow me to assume that the Antarctic has been isolated and washed by a cold sea for a very long time, probably over the entire Tertiary period (Andriyashev 1964).

Therefore, the representatives of the Antarctic ichthyofauna settled into very different ecological niches in the process of ecological development, and one branch of the subfamily Notothenieidae acquired white blood, a characteristic exceptional for fishes, which appeared in the Tertiary period (Andriyashev 1964). This feature evolved and formed several genera of the family Chaenchthyidae [Chaenichthyidae?] (Andriyashev and Tokarev 1958; Andriyashev 1964; Martsinkevich 1961; Regan 1914).

J. E. Permitin (1977) provided a detailed analysis of the ichthyofauna of the bottom fishes around the isolated oceanic islands of South Georgia and Kerguelen. He found that, in spite of the considerable endemism of each, the connection of the fauna of the bottom fishes remains substantial. Many authors (Andriyashev 1964, 1972; Permitin 1977; and others) consider that the [separation] of the populations of fishes and aquatic invertebrates took place in the past and probably continues nowadays because of the flow of the water mass of the Circumpolar Current. Since fluctuations in this water mass probably occurred in the past and take place now, there are links in the trophic connection of the fishes of both the Glacial and Kerguelen subregions. In the first place this must involve mollusks, which are the intermediate hosts. Generally, many groups of helminths show a great preference for them. In all probability the similarity of the helminthofauna of the fishes of this area must be explained by these features.

In respect to the endemism of the fauna of the parasitic worms, which is determined by the endemism of the ichthyofauna of both the Glacial and Kerguelen subregions, this phenomenon is also related to the Antarctic Circumpolar Current—which leads to the intensification of these circumpolar processes around the island and the submarine elevations. Local cyclonic systems are formed in these areas. Also, upwelling and the [consequent] enrichment of the shelf waters occur here. They cause a high biological productivity and play a great part in the formation of the local populations of the several species of fishes and of the endemic species of parasitic worms.

Interesting results were obtained by Gayevskaya and Kovaliova (1976) and Gibson (1976), who compared the trematode [digeneid] fauna on the Falkland-Patagonian shelf with that of the area around South Georgia and the South Orkney Islands where they reported 12 trematode species.

Representatives of the family Opecoelidae, which are absent from the shelf ichthyofauna, dominate in the basic fauna. Species of antarctic origin, such as *Elytrophalloides oatesi*, *Gonocerca trematomi*, and *Opechona magnatestis*, are detected in the trematode [digeneid] fauna of the Falkland-Patagonian shelf. This phenomenon is explained by the closeness of the Antarctic.

Thus, analysis of the helminthofauna of the fishes of the antarctic area has allowed us to establish a substantial uniformity in its composition and to reveal several features of the endemism in both the Kerguelen and Glacial areas and to establish the very insignificant relationship between the helminthofaunas of areas of the shelves of South Australia and Patagonia, adjacent to the Antarctic. In all probability these neighboring areas played no decisive role in its [the helminthofauna of fishes of the Antarctic region] formation.

Special Features of the Helminth Fauna of *Helicolenus maculatus* (Cuvier)

L. P. TKACHUK[1]

ABSTRACT

This paper presents special features of the helminth fauna of the fish *Helicolenus maculatus* inhabiting the area of Agulhas Bank and Walters Bank in the southeastern region of the Indian Ocean.

Helicolenus maculatus (Scorpaeniformes) is an industrially important species among purely sea [marine] fish. However, the literature contains little data about the helminth fauna of this species. A. M. Parukhin (1967) investigated *H. maculatus* in three regions of the Indian Ocean. In the area of Durban (Southeastern Africa) he noted 12 species of helminths. According to my data, the composition of the parasite fauna of *H. maculatus* in the Agulhas Bank area (Southern Africa) includes eight species. Only two of them, *Microcotyle caudata* and *Lecithochirum rufoviride*, are represented by pubertal helminths. More often the larvae of *Grillotia* sp. and *Anisakis* sp. inhabit the fish. They also exhibit the highest intensity of infection. Such a peculiar composition of parasite fauna is characteristic of deep-sea fish, to which *H. maculatus* is related. According to the literature, deep-sea fish are infected primarily by larval nematodes and cestodes, trematodes (Hemiuridae), and crustaceans. Adult forms of helminths are encountered very rarely. Noble (1973) arrived at this conclusion while investigating parasites of Macrouriformes fish from the eastern part of the Pacific Ocean. Earlier (Tkachuk 1980) it was noted that the greatest part of the helminthofauna of Zeiformes is composed of adults. This seeming disparity with the above-noted special features of the helminthofauna of *H. maculatus* can only be explained by the different depths inhabited by these species of fish. Thus, in the area of the Agulhas Bank, *H. maculatus* is caught in depths of from 200 to 400 m, and Zeiformes at depths of from 700 to 1,000 m. Another unusual feature of the helminth fauna of this area is a comparatively low infection by certain parasites, i.e., [the monogeneid] *Microcotyle caudata* (see Fig. 1).

For *H. maculatus* inhabiting the Walters Bank area, the characteristic feature is a smaller number of parasite species—seven, six of which are common. The larva of *Contracaecum* sp. (II), recorded only in this area, is the single exception. Except for [In addition to] the marked specific features indicated, there are considerably larger infections by such groups of parasites as Monogenea, trematodes [Digenea], nematodes, and crustaceans. However, the intensity of infection by them is considerably lower than that around the Agulhas Bank (Fig. 1).

Such essential differences of the parasite fauna of *H. maculatus* from the two areas being compared are connected with the peculiar features of its ecology. On Agulhas Bank the fish under study were caught from depths of 200-400 m, and around Walters Bank from depths of 700-800 m. Above all, this is based on the composition of their food. According to my data the main portion of the food of *H. maculatus* on the Agulhas Bank are Euphausiidae. Young individuals of deep-sea shrimps and fish are taken in lesser numbers. While in the area of Walters Bank, the bulk of food was young deep-sea shrimps and hermit crabs. The named species of [These] animals serve as bridging [intermediate] hosts of trematodes, cestodes, and nematodes, which is why their quantitative correlations in the food of the fish hosts defines the quantitative levels of infection by the different groups of helminths. Agulhas Bank is characterized by increased biological productivity of invertebrates, which brings about high intensities of invasion [infection] by such helminths as cestodes and nematodes.

The observed special features of the helminthofauna of *H. maculatus* (differences of the composition of helminths and of their quantitative levels of infection) show that we investigated [discovered] the different groups [populations] of *H. maculatus* inhabiting the areas around the Agulhas Bank and Walters Bank in the southeastern region of the Indian Ocean.

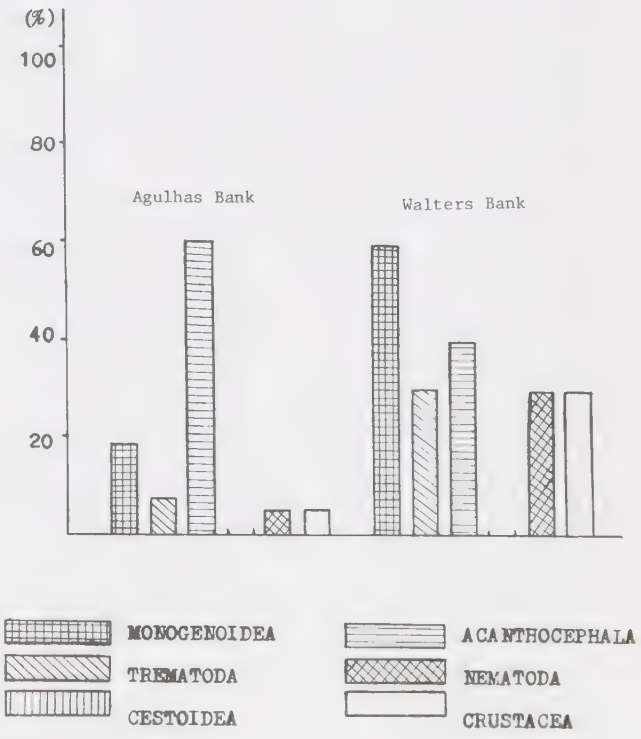

Figure 1.—Infection of *Helicolenus maculatus* (Cuvier) by groups of parasites.

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The Flatworm Fauna of Fishes of the Gulf of Mexico and its Genetic Relations[1]

E. V. ZHUKOV[2]

ABSTRACT

Host relations in "parasite-host" systems are considered with regard to lower monogenean and trematode [digenean] infection of fishes in the southern Gulf of Mexico. The prevalence of monohostal relations is established. The genetic relations of the fauna of the subject worms have been investigated and their Indo-West Pacific origin established. Lower monogeneans appeared to have a considerably higher evolutionary rate in comparison with trematodes [digeneans]. On the basis of fishes of the family Lutianidae, infected with monogeneans of the genus *Haliotrema*, the impoverishment of the ancient complex of these parasites in the process of evolution of their hosts is traced. The role of faunistic barriers in trematode distributions is discussed.

The fauna of the Gulf of Mexico has a complex genesis, interoceanic relations in the region of Central America having played a definitive role in its formation. Until the mid-Miocene they [the hydrographical features] permitted penetration of elements of the Indo-West Pacific tropical fauna into the newly formed basin. The coastal fish fauna of the Gulf of Mexico originated during the Cretaceous and became transformed considerably in isolation. Study of its parasites is of great interest.

I collected the flatworm material at my disposal in Campeche Bay and in the region of Havana during 1966 to 1968 and in 1974. To date, work on the lower monogeneans and trematodes [digeneans] from 391 specimens of 94 species of fishes has been completed. The cestodes, not yet worked up, are represented by larval forms.

Monogeneans of the subclass Polyonchoinea have been observed in 183 individuals of fishes belonging to 45 species. The percentage of infection of fishes by them in the open sea and in the coastal zone appeared to be similar (about 63%). The lower monogeneans are represented by 69 species, of which 57 (83%) are new. Worms of the family Dactylogyridae are predominant among them. It includes 48 species, 42 of which (87%) are new. The family Diplectanidae includes 19 species; 15 (79%) new ones. Two members of the family Capsalidae are noted. These data reflect the high degree of endemism in the lower monogenean fauna in the regions studied (Zhukov 1976, 1978, 1980).

The infection rate of fishes with trematodes [digeneans] was somewhat lower in the open sea than in the coastal zone (92% and 94%, accordingly). The fauna of this group is different from that of monogeneans. It is represented by 149 species (and 4 forms not identified to species) of which only 5 species (3.3%) were new. Out of 144 previously known species, only 85 (59%) are confined to the region of Central American seas, while the other 59 (41%) are known beyond this body of water.

A predominance of monohostal relations in the "parasite-host" system is typical of both groups of parasites. Among the lower monogeneans similar relations have been noted in 41 species (64%): Among digeneans of fishes of the coastal zone in 70 species (58%) and in the open sea in 42 (66%).

This is primarily a result of the prolonged existence of the above systems. For digeneans they are also a result of a narrow food specialization of the hosts under conditions of high intensity of biotic relations among members of the tropical ichthyofauna.

Analysis of digeneans occurring in fishes of the families Serranidae, Lutianidae, and Pomadasyidae, which provided the most abundant material for comparison, permitted me to distinguish species predominating in them. It has also shown that change in depth leads to redistribution of these forms and to a change in the species composition of trematodes. The presence of leading [predominating] species in the digeneid fauna of the above host groups suggests food specialization which leads to a reduction of competition between related members in every group. Cases in which similar species were found in the predominant forms of digeneans in different hosts have shown that such specialization does not permit them to avoid food competition completely.

Among the species discovered, *Metadena globosa* appeared to be predominant both for fishes of the family Lutianidae (*Lutianus apodus*, *L. synagris*, and *Ocyurus chrysurus*) and for a member of the family Pomadasyidae (*Haemulon plumieri*). For a number of digeneans (*Stephanostomum sentum*, *Leurodera decora*, and *Brachadena pyriformis*), obviously associated with fishes of the family Pomadasyidae, specimens occurring beyond this family are known. Thus, one may observe certain dynamics in relation to the historical groups of parasites along with their relations to certain systematic groups of hosts.

Analysis of the genetic relations of the above-mentioned flatworms has revealed their Indo-West Pacific origin and that the fauna of lower monogeneans beyond the barrier of the Isthmus of Panama appeared to have changed considerably more than the digeneid fauna, members of which have a complex developmental cycle. Of 69 species of lower monogeneans only 2 or 3% were common with the fauna of the Indo-West Pacific region (*Haliotrema similis* and *Diplectanum diplobulbus*) which allows me to regard them as the most ancient elements of the Gulf of Mexico. The Pacific host of the former parasite, *Priacanthus cruentatus*, remained in Atlantic waters where it existed in a stable condition and where the parasite transferred to the younger [evolutionarily newer or more recent] host, *P. arenatus*, endemic to the Atlantic Ocean. Another species, *Diplectanum diplobulbus*, parasitizing *Kyphosus cinerascens* in the Pacific Ocean, was found beyond the Isthmus of Panama in a phylogenetically younger host, *K. sectatrix*, also endemic to the Atlantic Ocean. These are examples in

[1]In this paper the word trematode means Digenea—an arrangement accepted increasingly by many Russian helminthologists and others.

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which components of the "parasite-host" system belong to different age periods, the host being younger in the evolutionary respect than the parasite.

Similar data have been obtained in the analysis of the distribution of monogeneans of the Indo-West Pacific genus, *Haliotrema*, among fishes of the family Lutianidae. Fish species in this family (of Indo-West Pacific origin) are endemics of the Atlantic Ocean and belong to the genera *Lutianus*, *Ocyurus*, and *Rhomboplites*, the latter two being monotypical ones. Since members of the genus *Lutianus* occur in the Pacific, I regard it as the most ancient. The genus *Ocyrus* has an amphi-Atlantic distribution. The genus *Rhomboplites* belongs among the endemics of the seas of Central America. The highest number of species of the genus *Haliotrema* was found in the most thermophilic members of the genus *Lutianus—L. machogoni* and *L. synagris* (six and seven species, respectively). Three species were found in *Ocyrus chrysurus*, and one in *Rhomboplites aurorubens*. No specific monogenean species were found in these phylogenetically younger hosts. Thus, we have an example of impoverishment of the ancient complex of gill parasites due to evolutionary changes of their hosts within a family. An analogous picture was observed in the monogenean species parasitizing fishes of the genus *Lutianus*.

The genetic relations of the digenean fauna of the Gulf of Mexico appeared to be wider. Among the 59 digenean species known beyond the limits of the seas of Central America and present in my material, 54 (91%) were found in the Pacific Ocean. Most significant are these connections with the fauna of the Central American Pacific coast where 45 (76%) of these 59 species occur (i.e., 31% of the total number of species of this group of parasites in my collection) and where 23 (51%) species among them are amphi-American endemics. Three factors are responsible for the high degree of these connections: 1) The relationship of hosts on the level of families and genera (but not species!), 2) interoceanic connections in the region of the Isthmus of Panama providing for exchange between faunas of the above bodies of water up to the Pliocene (2 to 5 million years ago), and 3) the conservatism of evolutionary processes in digeneans as compared with host species. One can derive an idea of the latter by comparing the faunas of both of the groups presently occurring on both sides of the Isthmus of Panama. Out of the 1,000 species of coastal fishes known from the basins being compared, only 12 (1.2%) have an amphi-American distribution (Briggs 1974). On the basis of data in the literature, I note 550 species of digeneans on them, of which 57 (10.3%) belong to the category of amphi-American species. Thus, the coefficient of divergence in the evolutionary rate of hosts and that of their parasites is equal to 10 in this case. Further study can only increase this index.

As concerns other regions, the digenean fauna of the Gulf of Mexico is most closely related to that of southeastern Asia where 18 common species are known (i.e., 30.5% of the group, or 12.5% of the total number of species analyzed).

Of particular interest are the connections with the digenean fauna of the coastal waters of western Africa. In my material, 13 species (9%) have an amphi-Atlantic distribution. Judging from the literature, 27 (5.4%) of the 499 digeneid species occurring both in Central American seas and off the coast of western Africa belong to the above category. Since the free-living period of larval digenean stages is very short, it appears impossible to conclude that their larvae are transported by extant currents from one region to another through the Middle Atlantic barrier. This phenomenon is of a deeply historical character and is associated with the existence in the far past (Upper Cretaceous) of a continuous range of the tropical fauna in the shelf zone which existed until the Brazil continental platform [plate] was separated from that of the African plate.

The data obtained from parasitological material have thus shown the error of the method for estimating efficiency of faunistic barriers proposed by the ichthyologist Briggs (1974). As has been calculated by the above author, the efficiency of the Middle Atlantic barrier is 91%. This value was obtained by comparing the total number of fish species of the tropical Atlantic shores (1,334) with the number of amphi-Atlantic ones (120, or 9%). The above method suggests trans-Atlantic (trans-Pacific) transfer of pelagic larvae from one region to another. Even ichthyological data contradict this view, as is shown by the fish fauna of Ascension Island, which consists of western elements to a high degree (30%) even though the Island is influenced by eastern currents from the coast of Africa.

Thus, parasitological data permit a new approach to understanding the amphi-Atlantic nature of the distribution of coastal fishes in the tropical Atlantic. Analysis of the studied digeneid fauna at the generic level has shown a still closer connection of the Gulf of Mexico with the above regions, since taxa higher than species are more significant in reflecting the pathways of faunal formation because they reflect, or demonstrate, more ancient relations.

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The Influence of Helminths on the Tissue Lipid Content of Black Sea Anchovy, *Engraulis encrasicholus ponticus*, and Bullhead, *Neogobius melanostomus*, During the Annual Cycle

A. M. SHCHEPKINA[1]

ABSTRACT

This paper presents data on the lipid content in tissues of Black Sea anchovy and bullhead at different infection intensity [levels of infection] by helminths during an annual cycle. A decrease in the lipid content of muscles and liver was noticed in heavily infected anchovy and bullhead. Helminths had the most influence on the triglyceride fractions.

Infection by helminths is an important factor influencing the status of fish populations in different seasons of the year. The struggle against helminths has become especially important due to the intensive development of freshwater fish-breeding and of marine and oceanic fisheries, as well as mariculture.

I planned to study the peculiarities of the lipid content of fishes with differing levels of invasion [infection] of helminths throughout an annual cycle. The research organisms chosen were the anchovy, *Engraulis encrasicholus ponticus* Aleksandrov, infected by larvae of the nematode, *Contracaecum aduncum* (3 to 1,200 individuals) and the bullhead, *Neogobius melanostomus* Pallas, infected by metacercariae of the trematode *Cryptocotyle concavum* (3 to 580 individuals). The qualitative lipid content was determined by thin-layer chromatography. The research was conducted on the livers and the white and red muscles of the anchovy and bullhead.

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The results obtained demonstrate impressive differences in the lipid content of heavily and lightly infected fishes during the annual cycle. These differences relate to the concentration values of separate lipid fractions and/or their relative content. Triglyceride concentration showed the greatest differences in all tissues of heavily and lightly infected anchovies and bullheads (Figs. 1, 2). The triglyceride concentration in white muscles of heavily infected *E. encrasiocholus ponticus* is lower by 33 to 71%; in red muscles by 37 to 57%, as compared with lightly infected *E. encrasciocholus ponticus*. Owing to the decrease in the triglyceride concentration, the total lipid concentration decreases in tissues of the heavily infected fishes as well (Figs. 3, 4). In the white muscles of the anchovy the difference is from 22 to 50%; in liver by 27 to 60%; and in red muscle by 9 to 34%. In liver of heavily infected bullhead the total lipid concentration is lower by 29 to 55%; in white muscles by 23 to 41% as compared with lightly infected fishes. Thus, helminths impact the reserve lipids primarily.

The degree of impact of helminths on the reserve lipids (triglycerides) of *E. encrasiocholus ponticus* and *N. melanostomus* is not

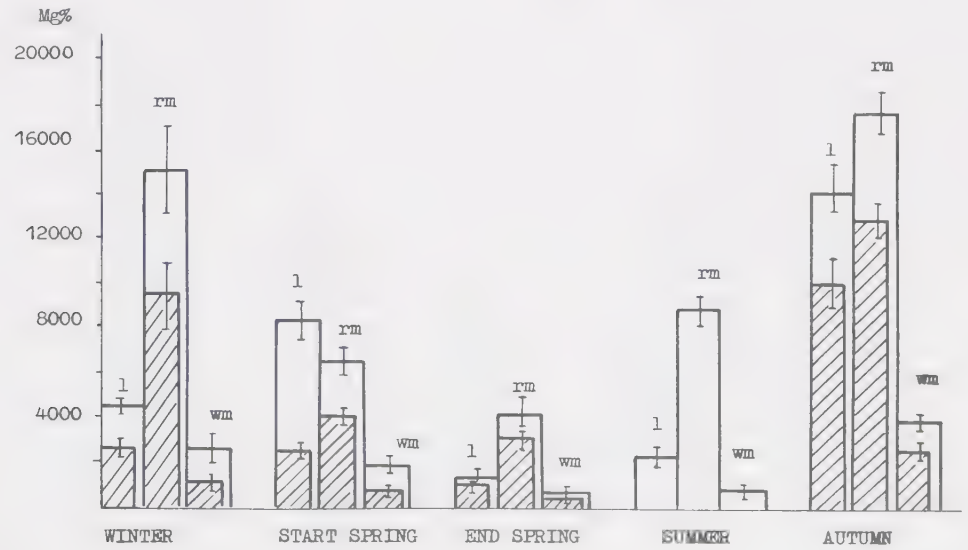

Figure 1.—Influence of *Contracaecum aduncum* infection on triglyceride concentration in anchovy tissues (mg%, wet mass): l = liver; rm = red muscles; wm = white muscles; open bars = weakly infected; hatched bars = heavily infected.

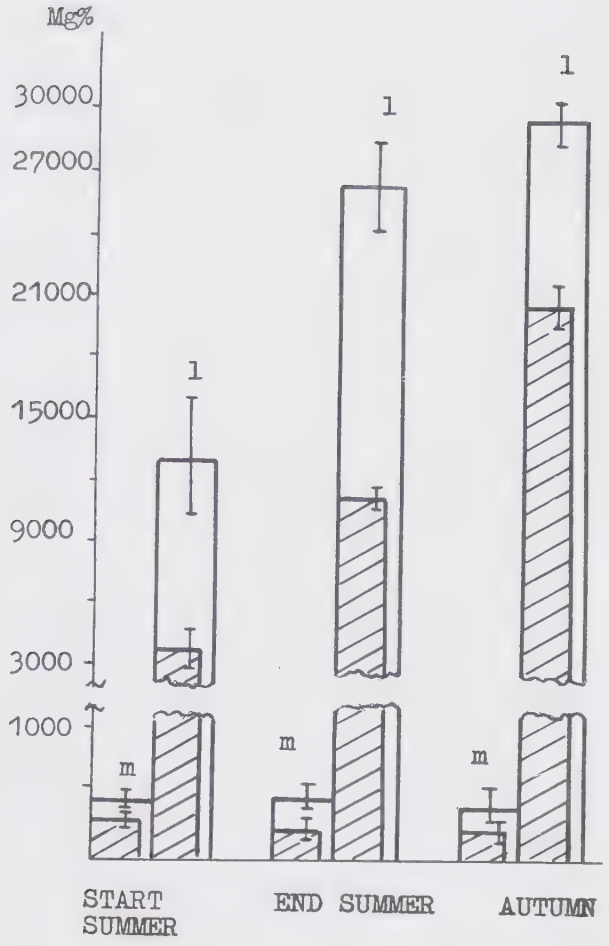

Figure 2.—Influence of *Cryptocotyle concavum* infection on triglyceride concentration in bullhead tissues (mg%, wet mass): m = muscles; l = liver; open bars = weakly infected; hatched bars = heavily infected.

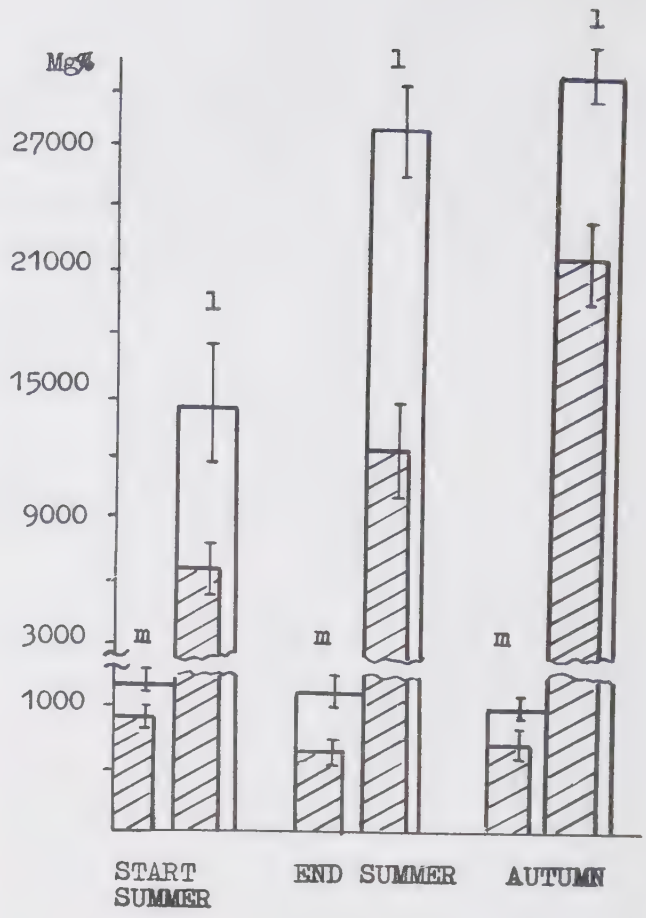

Figure 4.—Influence of *Cryptocotyle concavum* on summary [total] lipid concentration in bullhead tissues (mg%, wet mass): m = muscles; l = liver; open bars = weakly infected; hatched bars = heavily infected.

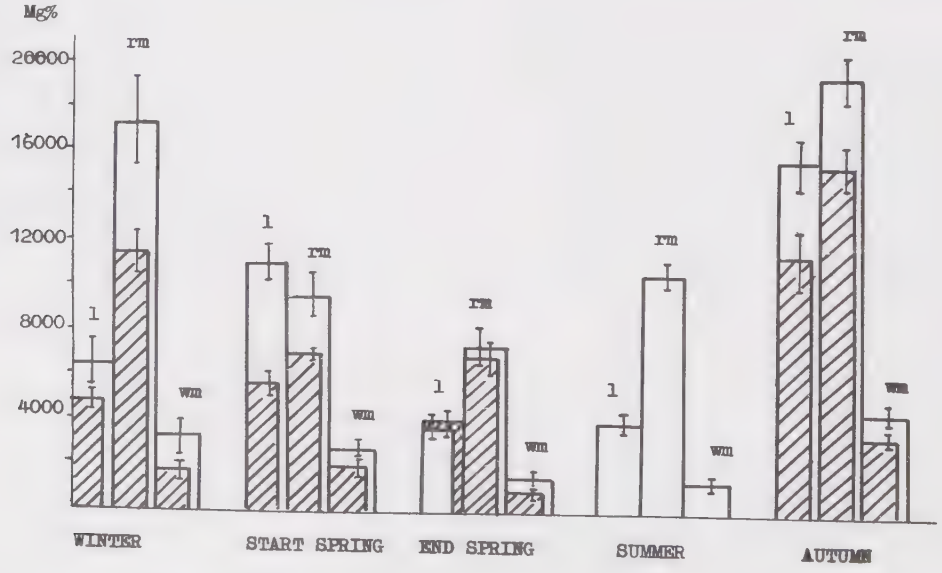

Figure 3.—Influence of *Contracaecum aduncum* infection on summary [total] lipid concentration in anchovy tissues (mg%, wet mass): l = liver; rm = red muscles; wm = white muscles; open bars = weakly infected; hatched bars = heavily infected.

identical for the different periods of the annual cycle. In contrast to triglycerides, the second fraction (by value) of phospholipids is not diminished in heavily infected fishes. And what is more, during the fattening period the phospholipid concentration in white muscles of the heavily infected anchovy is higher by 64%, in red muscles by 70%, and in liver by 42% ($P<0.01$). The livers of heavily infected bullhead demonstrated the same phenomenon during the spawning period. In other periods the phospholipid concentration is not distinctly different.

By reducing the triglyceride supply in anchovy and bullhead tissues, higher levels of helminth infection may cause an important effect on the physiological state of individual fishes in a population, on the state of the population and on the dynamics of their number as a whole. Helminth infection reduces the state of readiness of the anchovy for migration and wintering, influences the quantitative and qualitative characteristics for sexual maturation, reduces brood survival, and so on. Regarding the bullhead, except [in addition to] the foregoing effects, its condition for nest protection is reduced during the spawning period.

The data obtained allow me to assess the damage regarding the lipid supply. Thus, infection by helminths may [can] cause damage to the anchovy and bullhead populations. Such damage for the anchovy totals 25% and for the bullhead 20%.

Thus, the results show the important role of helminths in the substance/energy balance of large fishery populations in the Black Sea and, consequently, their important role in the ecosystems of that body of water. *Engraulis encrasiocholus ponticus* and *N. melanostomus* are the examples for this.

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Certain Results of the Study of Ciliates of the Family Trichodinidae (Peritrichida) Inhabiting Fishes of the Seas of the U.S.S.R.

G. A. STEIN[1]

ABSTRACT

This communication is a review of information on marine trichodinids (Ciliata, Peritrichida) in the seas of the U.S.S.R.

The first trichodinids found on marine fishes from reservoirs [waters] of the U.S.S.R. were identified as *Trichodina* sp. and *T. domerguei*. V. A. Dogiel (1940, 1948) suggested a number of taxonomic characteristics for their identification and established some separate species and subspecies and, in doing so, laid the foundation of the modern taxonomy of this group. The history of the study of marine trichodinids in my country may be divided into two stages: 1) The ciliates, collected together with other parasites of fishes, were identified from preparations stained with hematoxylin, and 2) since the end of the 1950's when the standard silver impregnation method came into use, special attention has been paid to parasitic ciliates parallel to the study of other parasites. Since that time the list of trichodinids has increased regularly.

The ciliates from the various bodies of the sea have been studied very sporadically. There are no data on Arctic Seas, except for the White Sea (Schulman and Schulman-Albova 1953; Stein 1976) and the Barents Sea (Polianski 1955; Stein 1973b). The first steps undertaken to study trichodinids from Far Eastern seas were by Dogiel (1948), Zhukov (1964), and Stein (1967, 1979). Information on trichodinids from the Baltic Sea involves only two very fresh regions such as the estuary of the Neva (Wu Bao-hua 1961) and the Gulf of Kurish (Stein 1982). More complete information was obtained on trichodinids of the Black Sea and the Sea of Azov by Stein (1975), the Caspian Sea by Ghasimegomedov (1970) and the Aral Sea by Osmanov (1976). Twenty species of trichodinids were found to occur only in saltwater, while 10 were found in fresh and brackish water.

Using identifications made on the basis of the standard silver impregnation method and taking into account the great interspecific variability of trichodinids, the number of species of trichodinids known from the Barents Sea is six. Also, 9 are known from the White Sea, 13 from the Black and Azov Seas, and 19 from basins of the Pacific Ocean, at present. Freshwater species of trichodinids prevail in the Baltic, Caspian, and Aral Seas. A small number of euryhaline species have been observed there. Truly marine trichodinids are absent from these bodies of water. Euryhaline *T. domerguei domerguei* and *T. tenuidens* were found in the coastal regions of the seas or in freshwater bodies near the sea coast. The largest number of marine trichodinid species has been observed in the Pacific Ocean basin. Comparison of the fauna of the Arctic, Pacific, and Atlantic basins disclosed a number of corresponding species: 7 of 19 in the White Sea and the Pacific Ocean and 5 of 19 in the Black Sea and the Pacific Ocean. A list of the marine and euryhaline trichodinids of fishes of the seas of the U.S.S.R. is provided in Table 1.

The following ecological groups of trichodinids were identified according to their geographic distribution and coincidence with fishes: 1) The thermophilic, cold-preferring and eurythermic species; and 2) the southern, northern, and widely distributed ones (Stein 1979). From the analysis of the data on trichodinid

Table 1.—Known marine and euryhaline trichodinids of fishes from the seas of the U.S.S.R.

1	*Trichodina arctica* Zhukov, 1964
2.	*T. californica* Davis, 1947
3.	*T. caspialosae* Dogiel, 1940
4.	*T. cottidarum* Dogiel, 1948
5.	*T. decipiens* Laird, 1961
6.	*T. domerguei domerguei* (Wallengren, 1897)
7.	*T. elegans* G. Stein, 1979
8.	*T. elegini* Schulman-Albova, 1950
9.	*T. frequentis* G. Stein, 1979
10.	*T. fultoni* Davis, 1947
11.	*T. galyae* Lom and Laird, 1969
12.	*T. hexagrammi* Zhukov, 1964
13.	*T. histicotti* G. Stein, 1979
14.	*T. inversa* Dogiel, 1948
15.	*T. jadranica* Raabe, 1958
16.	*T. jarmilae* Lom and Laird, 1969
17.	*T. lepsii* Lom, 1962
18.	*T. micromaculata* G. Stein, 1975
19.	*T. minima* G. Stein, 1979
20.	*T. miranda* G. Stein, 1979
21.	*T. oligocotti* Lom, 1970
22.	*T. oviducti* Polianski, 1955
23.	*T. ovonucleata* Raabe, 1958
24.	*T. pala* G. Stein, 1979
25.	*T. partidisci* Lom, 1962
26.	*T. ploveri* Zhukov, 1964
27.	*T. puytoraci* Lom, 1962
28.	*T. puytoraci marisalbi* G. Stein, 1976
29.	*T. raabei* Lom, 1962
30.	*T. rectuncinata* Raabe, 1958
31.	*T. suleimanovi* Ghasimagomedov, 1970
32.	*T. tenuidens* Faure-Fremiet, 1943
33.	*T. trichiuri* Dogiel, 1948
34.	*T. trigonofibulae* Zhukov, 1964
35.	(?) *T. luciopercae* Lom, 1970
36.	(?) *Paratrichodina incissa* (Lom, 1959)
37.	(?) *Tripartiella melanogrammi* G. Stein, 1961

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coincidence with different hosts it might be concluded that there is no narrow host-specificity in the majority of marine trichodinids. Fishes of the Order Perciformes prevail among the hosts of trichodinids. From these facts I suppose [or conclude] (Stein 1973a, 1979) that the trichodinids parasitized Perciformes fishes first and only later passed over to certain fishes of other orders.

Undoubtedly, further study of the ciliates of the family Trichodinidae from the seas of the U.S.S.R. will increase the faunistic lists of trichodinids and provide more exact ideas of their biology and ecology.

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Special Features of the Myxosporidian Fauna From Sea and Ocean Fishes

A. A. KOVALIOVA and S. S. SCHULMAN[1]

ABSTRACT

Regular research on Myxosporidia from open seas and oceans has been conducted by investigators of the following research institutions: The Zoological Institute of the Academy of Sciences of U.S.S.R., the Atlantic Research Institute, the Polar Research Institute, and the Pacific Research Institute.

As a result of this research a new myxosporidian fauna has been discovered. This provides a more complete idea of the order Multivalvulea and permits more precise definition of the marine Bivalvulea. Seven new genera and five new families have been established in the order Bivalvulea. The number of species has increased considerably.

The following problems are touched upon: The ways of adaptation of myxosporidian spores to living in different layers of the water body; the connection of different ichthyocoenosis in certain habitats of the ocean to their myxosporidian fauna; and the ways [paths] of migration of some Multivalvulea species from their initial dwelling place, the Indo-West Pacific, to the Atlantic. More evidence is presented on the evolution and phylogeny of the Myxosporidia.

Foci of infections and their agents are found in the Atlantic and, partly, in the Pacific Oceans. The species of fishes most infected with the genus *Kudoa* are revealed. Measures to control these infections are given.

Research on sea and ocean Myxosporidia is of great theoretical and practical importance. Analysis of the number of Myxosporidia species, their ecology and distribution among their fish hosts and in water aquatorias [water or ocean basins] has shown that these parasites originated in the seas. That is the reason species and genera with the most primitively constructed spores and most primitive vegetative forms occur only in the seas. Also, an exceptional diversity of myxosporidian forms is observed in the seas. This is mostly encouraged by the abundance of ecological niches.

Unfortunately marine Myxosporidia have been investigated poorly as compared with those in freshwater. Until 1941 only a few researchers studied Myxosporidia in the U.S.S.R. (Averinzew 1907, 1909, 1911, 1913; Dogiel and Bychovski 1939; Petruschevski 1932; Bazikalova 1932). Their works dealt with only a few myxosporidian species.

After 1945, new works on Myxosporidia appeared (Dogiel 1948; Schulman and Schulman-Albova 1953; Polianski 1955). Many were dedicated to the study of the entire fish-parasite fauna of the Soviet seas. This was of especial importance for the works of that period. Until 1970 only a few, but very interesting, works had appeared in the U.S.S.R. (Zhukov [1964?]; Naidenova 1968; Naidenova and Zaika 1969a, b; Zaika 1966, 1968). [A number has been published since; see Literature Cited section.]

Regular research on Myxosporidia from open seas and oceans has begun only in the last 10 yr based upon the three laboratories of Parasitology at three research institutes, i.e., the Atlantic Research Institute, the Polar Research Institute, and the Pacific Research Institute. This paper is dedicated to the results of these investigations, which is only the beginning of our efforts. First, we must provide the names of the researchers. They are: A. V. Gaevskaya, A. N. Zubchenko, A. A. Kovaliova, V. K. Krasin, and S. S. Schulman [see Literature Cited].

Investigations were conducted in the vast spaces of the Atlantic Ocean from Baffins Land and Greenland to the Atlantic waters, in the northern Pacific Ocean and in the open waters of its southeastern part. Unfortunately, the vast Indian Ocean has been very poorly investigated thus far. During this research more than 50,000 specimens of more than 350 species of fishes have been studied. This has permitted discovery of a new myxosporidian fauna.

When the order Multivalvulea was established by S. S. Schulman in 1959 it consisted of only 3 families, 3 genera, and 12 species. At present this order, owing to the works of Soviet protozoologists, numbers 4 families, 5 genera, and 40 species. Thus, we now have a more complete understanding of the order.

Studies of the more numerous [larger] order, Bivalvulea, have yielded data no less interesting.

Earlier certain researchers had reported on the interesting, aberrant, sea Myxosporidia, e.g., *Auerbachia*, *Parvicapsula*, *Unicapsula*, etc. Their systematic position and their importance in the Myxosporidia fauna were obscure. It has been found since that these species are members of fairly high taxa at the family level which show a particular trend in the evolution of Myxosporidia. For example, the genus *Auerbachia* is a member of the family Sphaeromyxidae which has the most primitive spores. This family consists of the initial genus *Spaeromyxa*, the genus *Auerbachia*, which originated from *Sphaeromyxa* (and has lost one polar capsule), and the genus *Meglitchia*, which was extracted from the genus *Ceratomyxa* and has not been completely described.

The origin of the genus *Parvicapsula* is not clear. The discovery of some new species belonging to this genus allowed us to trace the pathway of its evolution from the genus *Ceratomyxa*. Soon a new genus *Neoparvicapsula* was discovered and described. Thus, the most peculiar family Parvicapsulidae, consisting of two genera (*Parvicapsula* and *Neoparvicapsula*), was formed. The extremely interesting genus *Myxoproteus* stands apart from all other taxa, because of the unique structure of its spores. It has been shown that the two new genera *Bipteria* and *Schulmania* originated from this genus. The spores of *Bipteria* have two thin winglike processes; those of *Schulmania*, ventral and lateral keels. These three genera form the single family Myxoproteidae.

Moreover, two new families—Alatosporidae and Paliatidae—were established. The members of the family Alatosporidae, with their small polar capsules, are very much like those of the genus *Ceratomyxa*. But the spores of *Ceratomyxa* have a half-moon shape; while the spores of Alatosporidae are triangular and have two-winged appendices like *Ceratomyxa*. In the representatives of

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the second genus of this family, *Pseudoalatospora*, these appendices are twofold and are united at their anterior ends. It is quite evident that these structures promote [enhance] the ability of the spores to float in the water body [water column].

The monotypical family Paliatidae, whose hosts are deep-sea fishes of the family Alepocephalidae, is also very interesting. Its members have large spores with membranelike structures resembling parachute domes.

It must be noted that the new families and genera consist, as a rule, of 3 to 10 species. This provides evidence that the new families form a considerable part of the myxosporidian fauna.

The number of species of many genera described earlier have increased considerably. Only in the genera *Coccomyxa* and *Auerbachia* has the number of species remained static. These genera have few species and their representatives occur very rarely. Moreover, analysis of the three species of the genus *Auerbachia* has shown that they belong to a single, very variable, and widely spread species.

Though our studies on Myxosporidia are far from being completed, we can report more than 100 new species of sea Myxosporidia even now. New findings and revisions of previously described species allow us to add considerable detail, to reorder, and, in some cases, reevaluate our view on taxa described long ago. Thus, in such old and widely spread genera as *Myxidium* and *Ceratomyxa*, species were found with gigantic spores. In *Myxidium* they reach up to 100 μm, whereas their size does not exceed 10-20 μm usually. In *Ceratomyxa* they reach 740 μm (i.e., about 1 mm).

As previously mentioned, the spores of many sea [marine] Myxosporidia species develop various adaptive structures for floating in different layers of the water body [water column]. They are winglike and threadlike processes, membranes, keels, manthes, etc. The spores of some species of *Leptotheca*, *Sphaeromyxa*, and *Chloromyxum* have threadlike appendages and the spores of some *Davisia* species have large hornlike prolongations that can change into threadlike devices at their posterior ends.

The decrease of the size of the spores in the genera *Simuolinea*, *Chloromyxum*, and *Sphaerospora* also promotes slow-sinking of the spores. On the other hand, the size of the spore increases in some representatives of *Ceratomyxa*. This is due to the large hollow cavities within the mass of the spore, which decrease the specific weight of the spores, increasing their ability to float and promoting slower sinking.

At the same time the large size of the spores, as well as that of their polar capsules, increase the weight of the spores. That is why their occurrence in one or the other layer of the water body [water column] results from a range of oppositely directed factors. All these adaptations are of great importance for Myxosporidia living in seas and oceans, as their distribution is very extensive horizontally (area) as well as vertically (depth).

The spores of Myxosporidia move passively. Therefore, to be eaten [ingested] by their hosts, they must occur in the same part of the same water body [as those hosts]. *Ceratomyxa maxima* can serve as an example illustrating the influence of depth on the spore's size. Its spores, ranging from 470 to 740 μm, occur in *Berix* [*Beryx*?], which lives at depths of 800 to 900 m, while the spores of the some [same?] species ranging from 230 to 480 μm occur in the same fish host that lives at a depth of 240 to 400 m.

Thus, the enormous diversity of the shape and arrangement of sea myxosporidian spores promotes their adaptation to certain ecological conditions.

The distribution of fishes in the World Ocean is connected with their history as well as with their present life conditions. This has its reflection in the distribution of the Myxosporidia. Ocean fishes form icthyocoenoses which are related to certain dwelling areas; the main ones are the shelf zone, the continental slope, and the open ocean waters. Each has a very complicated structure.

The shelf zone includes ecologically d.fferent fish groups that are connected with the bottom, the pelagic zone, and estuaries. Neritopelagic forms can also dwell here. As a rule the most abundant fauna of Myxosporidia and the fishes most infected by them occur in these areas. The most numerous species, even those recently described, belong to genera described long ago. This is apparently because these sea [marine] areas have been the most completely studied.

The genera *Bipteria* and *Schulmania* are quite new and are found also in shelf waters. Their recency of discovery is due to their occurrence in areas never before studied (Baffins Land, Greenland, the Bering Sea, and the Sea of Okhotsk).

Adaptation of the spores of Myxosporidia of the shelf zone (i.e., whose waters are shallow relative to those of the deep sea) for floating occurs, but is not so striking. It is worthwhile mentioning that the members of the genus *Kudoa* and other representatives of the order Multivalvulea occur only in the shelf zone (i.e., in the zone of vertical raising of waters) [vertical movement or upwelling]. These vertical movements upward [upwelling] prevent the spores of the Multivalvulea, which are poorly adapted to floating, from sinking to the bottom. Unfortunately, many fish complexes of the shelf zone, particularly estuarine fishes, have not yet been studied.

The shelf zone passes directly into the continental slope zone where bottom, meso- and bathypelagic, nerito-oceanic, and epipelagic fishes live. The meso- and bathypelagic fishes are of particular interest. Thus, a new genus, *Paliatus* was found among representatives of this zone (family Alepocephalidae). Also, gigantic spores of Myxosporidia were found first in fishes of this zone.

Studies of the myxosporidian fauna of the open ocean were begun recently. Myxosporidia from fishes dwelling in submarine depths were studied. The myxosporidian fauna of ancient deep-sea fishes, particularly the family Macrouridae, is of the most interest. The majority of their Myxosporidia are dispersed throughout the World Ocean; some, e.g., *Auerbachia menatrosa*, *Myxidium coryphaenoides*, etc., are nearly cosmopolitan.

The myxosporidian fauna of pelagic fishes is not yet fully investigated. The first studies in the southeast Pacific have disclosed a small numerical strength of Myxosporidia species in this zone of the ocean.

Thus, 3 species of fishes [at least one belonging to the genus *Scomber*; the other(s) to other genera[2]] of the 14 well-studied ones were infected with 6 species of Myxosporidia belonging to 4 genera. The incidence of infection in these fishes was also very low. Some species of Myxosporidia have certain adaptations for floating. The other species are typical parasites of bathypelagic fishes and usually have adaptations for floating only in this horizon [or level]. Their occurrence in typically pelagic fishes is due to powerful upsurges [upwellings] of the water.

The theoretical importance of our research is not exhausted by the examples mentioned above. The following investigations [reviews or explanations] will be devoted to the genesis of water basins and their fauna. They will provide a clue to the solution of zoogeographical and biological problems. We now have more

[2]Only the name of the genus of one of the three species of fish was given in the original typescript. Its specific trivial name and the names of the other two species were not included.

precise data on the phylogeny of the Myxosporidia and the way [manner] of distribution of some taxa.

Thus, analyses of the distribution of the Multivalvulea have shown that they originated in the Indo-West Pacific. The most primitive species of this order, *Trilospora californica* (which lives in the gallbladder, the initial habitat of the Myxosporidia), is found only in this region, as are all known families and genera of the Multivalvulea. Moreover, the number of species is much greater here than in the Atlantic, in spite of a lower rate of studies in the Pacific. Lastly, the most numerous species of *Kudoa* have been found only in Pacific deep-sea fishes.

The order Multivalvulea is comparatively young. It arose after the formation of the present fish fauna of the Atlantic. Representatives of these Myxosporidia have a very typical local distribution. Hence, under these circumstances the penetration of numerous species of Multivalvulea into the Atlantic Ocean has been prevented.

Only 14 species of the genus *Kudoa*, 1 species of *Trilospora*, and 1 species of *Unicauda* were found in Atlantic fishes, and this was in spite of a much higher level of research on myxosporidians in this ocean.

Because macrourid fishes (and other ancient deep-sea fishes) have limited migration ability, only one species of *Trilospora* has penetrated into the Atlantic Ocean. Analysis of the number of Multivalvulea species and their distribution by fish hosts, indicates that these parasites could have arrived in the Atlantic by several different routes. The most probable one was from the Pacific Ocean around South Africa and its Atlantic shore. At present *Kudoa thyrsitis* occurs in the southeastern Atlantic. It occurs also in both the Pacific and Indian Oceans.

Kudoa clupeidae and *K. funduli* from [waters around] northwestern Africa are morphologically very similar to *K. nova* from the region of north Africa and the Mediterranean.[3] It is possible that *K. nova* has penetrated to the North American shelf by using such active migrators as *Thunnus* and Xiphidae. Here, this species may have given rise to *K. clupeidae* and *K. funduli*.

The *Kudoa* species occurring on the Falkland-Patagonian shelf, penetrated into the Atlantic via South America. Hydrographical barriers have prevented their migration to the north.

The *Kudoa* species found in the Gulf of Mexico do not occur in any other regions of the Atlantic. These species may have penetrated into the Gulf directly from the Pacific Ocean, before the junction of North and South America.

Finally, *Trilospora* from Coryphaenoides members of the mid-Atlantic ridge, apparently has penetrated directly with its host. Unfortunately, the pathways of invasion of this fish are unknown.

Investigations of Myxosporidia are of great importance for fisheries also. The Multivalvulea are not pathogenic to their fish hosts, but the fishery suffers great losses, some because certain species of this order reduce the quality of the flesh of infected fish. Others provoke lysis of the fish host's tissues even after prolonged freezing. This makes the fish unsuitable for food.

As a result of our studies in the Atlantic and partly in the Pacific, foci of infections and their agents were found; species of fishes infected with *Kudoa* were revealed; and the seasonal distribution of these parasites in some regions of the ocean was discovered. An instruction on how to utilize fishes infected with the genus *Kudoa* was provided on the basis of this research.

As the studies of recent years have shown, members of the Bivalvulea can be pathogenic also. Thus, *Henneguya* sp. can be pathogenic to fishes in aquacultural conditions.

Recently we have obtained from Dr. Hoffman[4] information on a new species of *Parvicapsula*, parasitizing the kidneys of pen-reared coho salmon, *O. kisutch*, which causes mortality of up to 30% of its hosts.

To search for measures to control these infections it is necessary to investigate not only the number of species, but also the biology of the agents.

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[3]The author may have meant "...from the northwestern Atlantic are morphologically very similar..."

[4]Believed by editor to be Dr. Glenn L. Hoffman of Fish Farming Experimental Station, U.S. Fish and Wildlife Service, P.O. Box 860, Stuttgart, AR 72160, U.S.A

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Myxosporidia of Fishes of the North Pacific

V. K. KRASIN[1]

Myxosporidians of fishes of the northern Pacific have been studied only recently. The first information about them was not published until the 1920's (Fujita 1923; Davis 1924).

By now a large number of works dedicated to Myxosporidia of fishes of that area have been published by foreign and Soviet scientists (Jameson 1929, 1931; Nobel 1938a, b, 1941, 1966; Moser 1976; Moser and Noble 1977; Dogiel 1948; Polianski 1958; Zhukov 1964; Schulman 1966; and others).

As the result of these studies new species of Myxosporidia have been registered [recorded] and the number of hosts for previously known species has increased. In addition, information on taxonomy, problems of ecology and development, and the relationships between parasites and hosts have been covered. Many interesting works deal with the spatial and seasonal distribution of *Myxosporidia* in the ocean and their dependence on biotic and abiotic conditions as well as the influence of Myxosporidia on the fish hosts, themselves.

Since 1972 the TINRO Laboratory of Parasitology of Marine Animals has conducted planned investigations of Myxosporidia of fish of the northern Pacific.

Thus far, 1,809 fish belonging to 43 families, 81 genera, and 132 species have been studied. In our collections 41 species of Myxosporidia were new and 65 were found for the first time in new hosts, while 12 were not identifiable as to species because of an insufficient number of spores.

In all, a total of 190 Myxosporidia have been registered [recorded] from the North Pacific, according to our data and that from the literature. One hundred and twelve species of Myxosporidia were found off the Asian coast—96 of them belonging to the order Bivalvulea and 16 to the order Multivalvulea. Myxosporidia of the genera *Ceratomyxa* (26 species), *Myxidium* (19 species), *Kudoa* (14 species), and *Chloromyxum* (11 species) were most abundant.

Eighty-seven species were registered in the northeastern Pacific, 75 of them from Bivalvulea and 12 from Multivalvulea. The genera *Ceratomyxa* (18 species), *Myxidium* and *Kudoa* (10 species, and *Leptotheca* (9 species) were predominant as well as in the northwestern Pacific.

In both areas 18 genera from 9 Myxosporidia families were registered [recorded], but myxosporidians of the genera *Auerbachia* and *Unicapsula* were not found in the northwestern Pacific while those of the genera *Sphaerospora* and *Hexacapsula* were not found in the northeastern Pacific.

The faunal similarity of Myxosporidia of the shelf fish of these areas at the species level is insignificant. It is interesting to note that there are no common species of the order Multivalvulea parasitizing mainly [primarily] shelf fish in the Pacific waters off the North American and Asian coasts.

The Myxosporidia fauna of bathyal fishes has been studied much less than that of shelf fishes. Nevertheless, available data on the infection of *Coryphaenoides* spp., *Laemonema longipes*, and *Anoplopoma fimbria* allow us to state a somewhat closer species similarity of Myxosporidia in the given areas.

Even my incomplete data (materials on bathyal fishes received in 1980 are still being processed) indicate that 10 species of Myxosporidia have been found to be common in these areas (i.e., *Myxidium coryphaenoidium*, *M. melanocetum*, *M. pearcyi*, *M. melanostigmum*, *Ceratomyxa anoplopoma*, *C. obesa*, *C. asymmetrica*, *C. coryphaenoida*, *Davisia anoplopoma*, and *D. coryphaenoida*).

Myxosporidia of the other Multivalvulea, which cause considerable economic losses to the fish industry due to impairment of the market value of the fish (even rendering the fish unfit for human consumption in some cases), have drawn the greatest attention.

Three years ago more than 40 species of multivalvular Myxosporidae were known. They were divided into four families, i.e., Trilosporidae, Kudoidae, Pentacapsulidae, and Hexacapsulidae (Kovaliova and Schulman 1978). According to my data, 27 species of Multivalvulea of three families (Trilosporidae, Kudoidae, and Hexacapsulidae) are registered [recorded] from the North Pacific.

By now a total of 50 species of multivalvular Myxosporidae have been registered [recorded]. Two genera have been placed in the family Trilosporidae: *Unicapsula* (one species) and *Trilospora* (two species) were found, *Trilospora californica* in the gallbladder and *Trilospora* [sp.?] in the muscles. The family Tetracapsulidae is represented by the 23 species of the genus *Kudoa*. *Kudoa perecardialis* was found in the pericardial cavity of *Seriola quinqeradiata*. The other species were located in the muscles of the fish. The family Hexacapsulidae contains one monotypic genus, *Hexacapsula*, found in the muscles of *Neothunnus macropterus*. The representatives of the other above-mentioned parasites have been found in 25 species of fish. The muscles of the following fishes are most greatly infected by Myxosporidae of the genus *Kudoa*: *Merluccius productus* (two species), 124 specimens of 151 examined were infected (85.2%); *Engraulis mordax*, 159 from 225 fish specimens (70.6%); *Coryphaenoides pectoralis*, 34 infected fish specimens of 66 investigated (51.5%); *Atheresthes evermanni*, 15 infected fish specimens of 56 examined (26.8%); *Hippoglossoides elassodon*, 6 infected fish specimens of 33 studied (18.2%); and *Coryphaenoides cinereus*, 5 infected fish specimens of 30 examined (16.6%).

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Investigations of the Ultrastructure and Cytochemical Peculiarities of *Kudoa quadratum* (Thelohan, 1895), (Myxosporidia, Multivalvulea)

A. V. USPENSKAYA[1]

ABSTRACT

The ultrastructure, mode of nutrition, and host-parasite relations in *Kudoa quadratum* (Myxozoa) from muscle fibers of *Myoxocephalus scorpius* are discussed.

The ultrastructure and cytochemical peculiarities of *Kudoa quadratum*, a parasite of muscle cells of *Myoxocephalus scorpius* from the White Sea, were studied (Figs. 1, 2, 3). *Kudoa quadratum* is an intracellular parasite. Vegetative stages of *K. quadratum* and the so-called "cysts" have nothing in common with the resting or reproductive cysts of other Protozoa. *Kudoa quadratum* has a rather large (up to 2 × 0.3 mm) fusiform plasmodium bounded by a unit membrane. Usually one can see remnants of protofibrils between the membrane of the plasmodium and the muscle cell membrane. Plasmodia utilize the protofibrils by phagocytosis or by pinocytosis after lysis of the latter. Alkaline phosphatase was discovered at the surface of plasmodia. The cytoplasm of the trophozoites is rich in glycogen. There is no succinat degidrogenase [succinate dehydrogenase?] activity in trophozoites. It seems that trophozoites are anaerobic organisms and that glycogen is a principal source of energy for them. The development of the trophozoites and sporogenesis take place inside one and the same muscle cell. I did not observe ruptures of muscle cell membranes as a result of infection. Only one plasmodium can be observed inside each infected muscle cell. The muscle fibrils adjoining the infected one seem to be undamaged if the trophozoite is not too large.

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Figure 1.—The spore of *Kudoa quadratum* with four valves and four polar capsules.

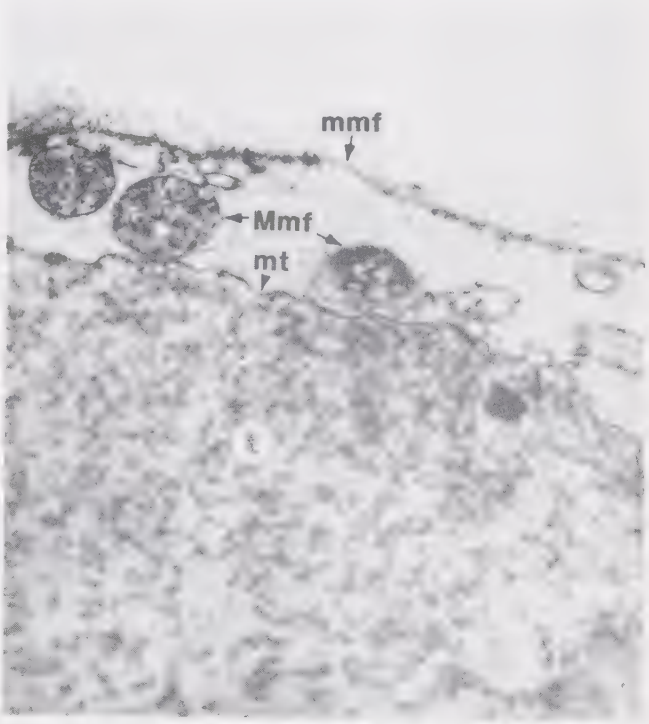

Figure 2.—Trophozoite of *Kudoa quadratum* (t) inside muscle fiber. mmf = membrane of muscle fiber, mt = trophozoite membrane, Mmf = mitochrondria of muscle fiber.

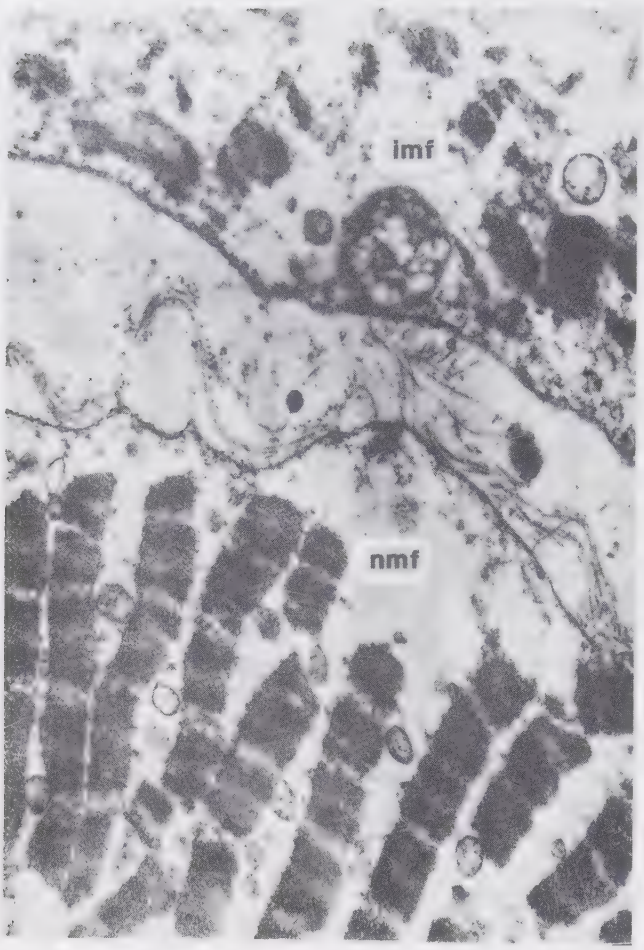

Figure 3.—Ultrastructure of infected (imf) and noninfected (nmf) muscle fiber.

Trematodes of Commercial Fish of the Pacific of Practical Importance[1]

V. D. KOROTAEVA[2]

Trematodes [digeneids] belong to the most numerous group of flatworms, with a considerable number being parasites of marine fishes. The total number of known trematode species invading marine species at different stages is about 3,000 species belonging to approximately 700 genera (Kurochkin in litt.). Many of them are of great importance to marine ecosystems, though this aspect of marine parasitology requires further study. My attention is primarily attracted by those trematode species of greatest practical significance.

The adult or larval forms of such trematode species are highly pathogenic for fish and may affect their number, reduce the quality of raw fish and fish products, or be harmful to a human being [and a few may infect humans]. [Hence, trematodes may be harmful (economically and medically) to humans.]

In this paper I shall review the most important trematode species of Pacific marine fishes encountered by commercial fishery specialists. These materials have been obtained while processing trematodes of commercial marine fish collected by specialists of the Laboratory of Parasitology of Marine Animals of TINRO from the different parts of the Pacific Ocean. Data concerning the level of infection of fish by the above species and the forms of trematodes are presented as well.

Commercial fish whose muscles are infected by trematodes are observed in almost all areas of the Pacific Ocean. Metacercariae of trematodes of the family Acanthocolpidae Luhe 1909 are frequently recorded from marine fishes. Sometimes they invade the muscles under the skin or the fins in great numbers, thus making some fish catches unmarketable, which results in considerable economical losses.

Metacercariae of *Stephanostomum* spp. have been observed in 29.5% of the fish examined (of 12 fish species) in the northwest Pacific. They were found on 6.9% of fish (three fish species) in the northeast Pacific; 54.5% (four fish species) in the Hawaiian area; 10.8% (two fish species) in the Philippine Sea area; and 51.6% (six fish species) in the Australia-New Zealand area.

The highest level of muscle infection has been observed by TINRO specialists on [several] flatfishes of the northwest Pacific, i.e., *Lepidopsetta biliniata* (39% at an intensity of up to 101 individuals), *Limanda aspera* (58.5% at an intensity of up to 25 individuals), and *Hippoglossoides elassodon* (20.4% at an intensity of up to 38 individuals).

Such high levels of infection off the Asian coast may be attributed primarily to the greater availability there of continental shelves and slopes where fish have more chances of becoming infected from benthic invertebrates—the first intermediate hosts of these trematodes.

On the basis of data in the literature, I recorded six larvae of the genus *Stephanostomum*, which were identified to the species level, on various fishes of the World Ocean. Considering the still imperfect specific criteria of trematodes of this genus and the great number of species described to date (more than 70), it is natural to admit significant difficulties in their determination [identification]. I am of the opinion that it is impossible to refer [utilize] the nomenclatural and systematic changes offered by Dollfus (1972) for the genus *Stephanostomum*, since it would increase the confusion. I (Korotaeva undated) described some larval forms of metacercariae of the family Acanthocolpidae from the muscles of certain marine Pacific commercial fishes.

Larvae of trematodes of the family Bucephalidae Poche, 1907 are of no less importance from a practical point of view. Larval *Prosorhynchus crucibulus* were observed in the northwest Pacific in the muscles and under the skin of 13.9% of fish of seven species including *Myoxocephalus jack* (66.7% of fish at an intensity of up to 7 specimens), *Sebastes alutus* (56% at an intensity of up to 142 specimens), and *Melletes papillio* (50% at an intensity of up to 30 specimens) revealed the highest level of infection. The highest intensity of infection, up to 1,000 specimens, was observed in *Hexagrammos lagocephalus*. According to the literature, 17 Pacific fish species are known to have their muscles infected by larvae of this species. Additionally, metacercariae of seven species of trematodes of the family Bucephalidae were registered on various benthic fishes of the World Ocean.

Larvae of trematodes of the family Didymozoidae Poche, 1907 are widely distributed among oceanic fish. They are observed in different organs and tissues. Their location in the muscles is quite common for fishes of the tropical and subtropical Pacific. Around Hawaii they are found in 75% of *Epinephelus guarnus* at an intensity of from one to two specimens. Fourteen percent of *Ocycrius japonica*, at an intensity of one specimen are observed to be infected in the Philippine Sea. Forty percent of *Saurida undosquamis* at an intensity of up to 10 specimens, 33.3% of *S. tumbel* at an intensity of up to 23 specimens, 40% of *Pentapodus senosus* at an intensity of up to 10 specimens, and 75% of *Pristipomoides typus* at an intensity of from one to five specimens were found infected off northern and northwest Australia. In the New Zealand area, 5 specimens of the trematode were observed in 1 of 35 individual *Nemadactylus macropterus*.

The helminthological literature presents data concerning localization of some adult didymozoids in the muscles of the large pelagic fish. Large envelopes with cyst formations containing eggs of already degenerated adult didymozoid species are often observed in their muscles. Mature trematodes, *Nematobothrioides australiensis*, were described by us (Nikolaeva and Korotaeva 1970) from *Scomber australasicus* from the Great Australian Bay. They are localized in the gonads of females, where their [period of] intensive maturing coincides with the spawning period [of the host].

[1]As used here the word trematode means Digenea, as is now widely accepted by Russian scientists.

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Trematodes of the species *Gonocerca ashoro* (family Derogenidae) have a similar microhabitat, locating in the ovaries of females of *Nematonurus pectoralis*. These trematodes reach 3 cm in length. They are of bright brown color and easily visible among the eggs, and may hinder marketing of this valuable product. They were registered [recorded] by TINRO specialists in the area of the Emperor Range on 13.3% of fish with an average invasion [infection] of up to four specimens.

In the North Pacific we found an interesting phenomenon of localization of the trematode *Aporocotyle theragrae* in the muscles of 48 of the 1,937 *Theragra chalcogramma* studied (2.5%), at an intensity of up to 76 specimens. Such abnormal location of these trematodes may be explained by the fact that some larvae begin growing after penetration into the small blood vessels of the host and are not able to get into the larger blood vessels—their normal location. Their size may reach that of adult trematodes, but sexual maturity never occurs in this location and they perish, degenerate, and become calcified. In addition this fish, primarily its muscles, are infected by two species of metacercariae of trematodes of the family Cathaemasidae whose definitive hosts are birds.

Metacercarial *Liliatrema skrjabini* were observed in eight fish species and *L. sobolevi* in one fish species.

Among trematodes recorded as being in the muscles of marine fish, I know of only one species, *Nanophyetus salmincola*, which is of definite medical importance. It usually infects salmonids in freshwater, but the metacercariae are able to survive in the muscles of anadromous fish while they are in the ocean. When in the human intestine, the live metacercariae leave the cysts and grow to be mature trematodes, thus causing a disease—nanophyetosis, which is not very dangerous but is unpleasant. As indicated, *N. salmincola* is a parasite of freshwater origin. No marine trematode species found in fish muscles are known to be pathogenic to humans.

Metacercariae of trematodes located in fish muscles are usually found in specific hosts, though not so regularly as is the case with maritae. Therefore, infection by them is not observed on all ichthyofaunal components within any area of the sea but may be found only in particular commercial fish species. From the practical point of view this allows us to determine the commercial fish species whose muscles are always free from invasion, as well as fish which require constant or episodical [specific?] parasitological control for human consumption purposes.

I must indicate that I consider that nearly all known incidents of rejection of marine fish catches during the last 15 yr because of trematode infections were groundless. In all these cases the parasites infecting the fish were not harmful for human beings and the level of infection, except in some rare instances, was not sufficiently high to cause loss of marketing quality. The skill of the persons conducting the parasitological inspections was inadequate.

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Infestation Rate of the Young of White Sea Herring, Reared Under Experimental Conditions and Caught in the Sea, by Trematodes, and Their Pathogenic Effect [1,2]

O. F. IVANCHENKO and T. A. GROZDILOVA[3]

While rearing White Sea herring we observed deaths of larvae infected by trematodes of the family Hemiuridae, *Brachiphallus crenatus* (Rudolphi 1802) and *Lecithaster gibbosus* (Rudolphi 1802), located in the digestive tract. Presence of *B. crenatus* resulted in injury of the mucuous membranes hindering the passage of food, causing embolism of the intestine and inhibition of the growth of larvae and fry (Ivanchenko and Grozdilova 1971). *Lecithaster gibbosus*, actively moving in the digestive tract of the young by means of their suckers, injured the mucuous membrane of the intestine. As a result, the larvae and fry ceased feeding and died (Ivanchenko and Grozdilova 1971). These two trematode species, pathogenic for herring larvae and fry, were primarily responsible for the deaths of the young in the aquarium [experimental containers]. Their pathogenic influence is apparently the same in nature. Therefore, we have begun a study into the infestation rate of herring at early stages of ontogenesis under experimental conditions and in nature. In 1979 work was performed on herring inhabiting the Chupa Inlet of Kandalaksha Bay in the White Sea. Under experimental conditions, hatching of the larvae occurred on 5 June. Larvae were fed with plankton caught in the sea. Four hundred and thirty larvae and fry of herring studied during the period of rearing contained two species of trematodes, *B. crenatus* and *L. gibbosus*. The first parasites were noted on 2 July. The number of parasites was one to two per larva, the percentage of infestation being 4%. The percentage of infection by both trematode species increased to 10% by 11 July, to 30% by 23 July, to 52% by 30 July, to 58% by 7 August, and, at the end of the experiment on 13 August, it was 68% with the intensity of infestation being one to three parasites per single young fish.

Abundant hatching of larvae in nature occurred at approximately the same time as in the experiment. The first larvae with parasites (*B. crenatus* and *L. gibbosus*) were discovered on 9 July. The percentage of infestation [infection] attained 8.2%; on 17 July it became 57%; on 26 July it was 76%. The latest [for the year] collecting in the sea was performed on 3 August. The percentage of infection was 67%, with an intensity of infection in the digestive tract of one to five specimens per individual juvenile. The results suggest that infestations of White Sea herring at early stages of ontogenesis under experimental conditions and in nature are synchronous and fluctuate within approximately the same limits.

Apparently, the dynamics of infestation of the young reared in aquaria can reflect infestation of larvae and juveniles in the sea to some degree. Experimental conditions make it possible to estimate relatively precisely the percentage of herring killed by the above parasites. Such calculations would be impossible in nature. Thus, artificial rearing permits a more detailed study of the influence of trematodes occurring on larvae and fry, and provides an idea of the degree of pathogenicity of these parasites for herring young in nature.

[1]As used here the word trematodes means Digenea.

[2]No Literature Cited section was supplied by the authors.

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Trematodes—Didymozoidae Fauna, Distribution and Biology[1]

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ABSTRACT

Questions on the specific structure [organization] of the family Didymozoidae, represented by 212 species, are considered. More than 100 species of fishes have been registered [recorded] as hosts of didymozoid maritae. The geographical distribution of didymozoids is analyzed and their connection with tropical and subtropical zones of the World Ocean is disclosed. An analysis of didymozoid development cycles is made according to the scheme of the trophic relations of the fish involved.

The maritae of trematodes of the family Didymozoidae (Monticelli, 1888), Poche, 1907 parasitize marine fishes mainly, rarely freshwater ones. Metacercariae are recorded from fishes, squids, crustaceans, and other invertebrates. The study of Didymozoidae began in 1819 when C. Rudolphi described the first species. The history of the study of the didymozoids has been well described by K. I. Skriabin (1955) and supplemented by me (Nikolaeva 1975). The greatest number of didymozoid species has been described by S. Yamaguchi—4 species in 1934, 16 species in 1938, and 68 in 1970—in all 115 species of Didymozoidae.

Descriptions of 200 species have been published to date. Study of the numerous didymozoid collections at our disposal (collections of IBSS, TINRO, and others) disclosed many new species from all regions of the World Ocean. They represent different subfamilies. I studied and described 40 didymozoid species. Twenty-seven (or 67.5%) new ones were referred to eight subfamilies. The descriptions of 12 new species have not been published yet.[3] I have adopted the didymozoid system of Yamaguchi (1971). Thus, at present, the family numbers 212 species placed in 81 genera and 23 subfamilies (Table 1). The systematics of the Didymozoidae is in a chaotic state. A number of species, genera, and subfamilies differ [only] by very insignificant characters. At the same time, species with quite different morphology are sometimes united into one genus. Analysis of the subfamily Koellikerinae (Nikolaeva 1978) allowed me to reestablish the competence and validity of the genus *Wedlia* Cobbold, 1860, and reduce the genus *Tricharrhen* Poche, 1925 to synonymy. Further work on the collection of trematodes of this subfamily confirmed the correctness of my point of view.

New representatives of this subfamily have been described. The discovery of a new species of the genus *Koellikeria* is especially interesting (Fig. 1). The type species, *K. okeni*, was described in 1860 and for 120 yr it has been the only representative of this genus and a new species of the genus [*Koellikeroides* sp.] appears to be unusual. Together with specimens having the usual sex ratio (1:1) [ratio of sexes], I found specimens with two or three males inside a single female. In this case the males are situated, not in a central cavity groove, but penetrate deep into the female's body [Figs. 2, 3].

Since the systematics of Didymozoidae is only now being worked out, Mayr's expression (1971:83) is quite correct [and applies]: "In groups where an inventory is still in full swing and when exceptions are too-poor local populations, it is difficult to apply the methods of population system" [systematics].

Analysis of the geographic distribution of didymozoida is difficult. The difficulty lies primarily in the fact that the fish to be examined often have been bought at a market and the site where they were captured is not recorded or known. Second, in some regions of the World Ocean fish infections (by didymozoids) are

Table 1.—Systematics of Didymozoidae.

N/N	Subfamilies	Number	
		Genera	Species
1	Didymozoinae	21	79 (3)[1]
2	Adenoididymocystiinae	1	1
3	Annulocystiinae	2	2
4	Colocyntotrematinae	1	2
5	Didymocodiinae	2	2
6	Glomeritrematinae	1	1
7	Gonapodasmiinae	3	14
8	Koellikeriinae	4	19 (2)
9	Metadidymozoinae	1	1
10	Nematobothriinae	23	52 (6)
11	Neodidymozoinae	4	4 (1)
12	Neodiplotrematinae	1	1
13	Nephrodidymotrematinae	1	1
14	Opepherocystiinae	1	1
15	Opepherotrematinae	4	4
16	Osteodidymocodiinae	1	1
17	Patellokoellikeriinae	1	1
18	Phacelotrematinae	1	1
19	Philopinninae	2	3
20	Pseudocolocyntotrematinae	2	3
21	Reniforminae	1	1
22	Sicuotrematinae	1	1
23	Skrjabinozoinae	2	2
	Genera not placed in subfamilies		3
		81	200 (12)
			212

[1]The parentheses contain data on new species as yet unpublished. [At the time the textual manuscript was submitted to the editor in the fall or winter of 1981.]

[1]As used here the word trematodes means Digenea.

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[3]At the time the textual manuscript was provided to the editor in late fall or winter of 1981.

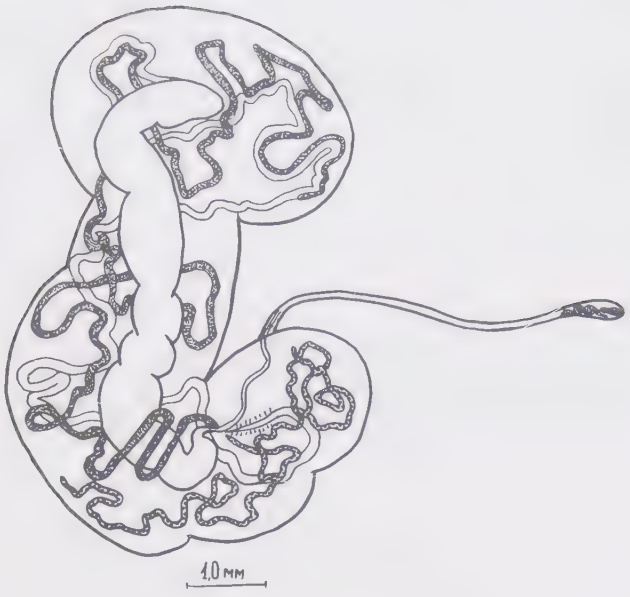

Figure 1.—*Koellikeria* sp.

Figure 2.—*Koellikeroides splenalis* Nikolaeva.

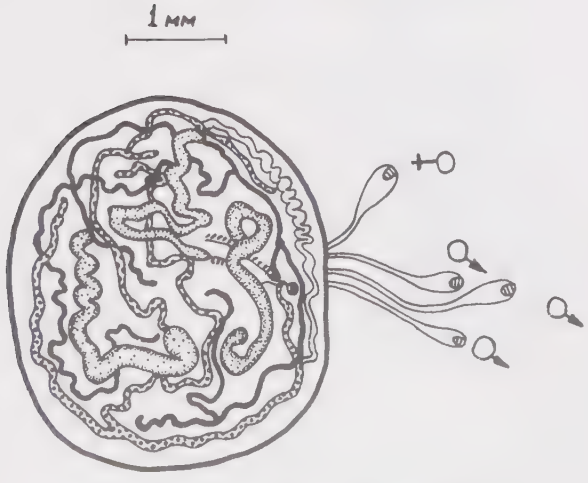

Figure 3.—*Koellikeroides splenalis* Nikolaeva.

only poorly known, or there is no information at all (as in the region of the Indo-Malayan Archipelago). Nikolaeva (1970, 1978) has already noted that didymozoids occur in tropical and subtropical zones of the World Ocean. In the oceans [known] didymozoids are distributed as shown in Figure 4. Five species have been described from freshwater. Two species were found in the Nile, and one each in the Laohe River (the basin of the Yellow Sea), in the rivers of Japan and the U.S.A. (the States of Louisiana and Oklahoma).

The didymozoida fauna is abundant and varied in the Pacific Ocean. The greatest number of species (84 of 143) is registered [recorded] in the region of the Hawaiian Islands (Yamaguchi 1970). Yamaguchi pointed out that the Hawaiian Islands lie in the watershed of the West-Indian Pacific zoogeographic region. Forty-seven species are found near the coast of Japan in the Sea of Japan and from the ocean side [of the islands of Japan] and only 19.9% of them are common with Hawaiian ones. Eight species are found in an open part of the [Pacific] ocean. Three species were collected in the California region and one near the Mexican coast. Single species are noted in the Philippines and Makassar regions and in the Arafura Sea.

The Indian Ocean didymozoida fauna had but five species and was "a blank spot" [void] before my investigations. Forty-nine didymozoida species are registered there now. Twenty-seven species of didymozoida were collected from seven host species in the Comoro Islands region. There are seven species in the Gulf of Mannar and five around the Agulhas Bank. Three species are recorded from the Great Australian Bay and in the tropical ocean zone. Two species are found in the Red Sea, by one [and one each] in the Cape Guardafui region, near Safala Bank, and the Indian coast. Forty-nine didymozoid species are registered from the Atlantic Ocean basin, 32 species are from the ocean, 23 from the Mediterranean Sea, and 2 from the Black Sea. The greatest number of species in the Mediterranean Sea is noted near the coast of Italy and in the Adriatic Sea. Solitary didymozoida are found near the coast of Algeria, Morocco, and in the Suez Canal.

Didymozoida are found in the following regions of the Atlantic itself: 13 species in the Gulf of Mexico and near the Florida coast; 2 species in the Bermuda region and near the coasts of England and Sweden (in the North Sea). There was one species [each?] in the Kurasao [Curacao?] region, in the Guinea Gulf [Gulf of Guinea], and in the south and southeast Atlantic. Exact coordinates are lacking for the 14 species recorded from the Atlantic Ocean.

To secure an idea of the distribution of didymozoida in the World Ocean I employ the information on didymozoids from the collections on which I have not yet worked. The most abundant collections of didymozoida of the Pacific Ocean were made in tropical waters (126 infected fish specimens). In the Northern Hemisphere didymozoida are registered in the Hawaiian Islands region (15 fish specimens), near California (on 10 fish specimens), near the coast of Mexico (on 8 fish specimens), in Teuantepek Bay (on 4 fish specimens), on the coast of Japan (on 1 fish specimen), in the Philippines region (on 7 fish specimens), in the northeastern part of the South China Sea (on 30 fish specimens) and in the New Zealand region (on 21 fish specimens), in the Tasmanian Sea (on 1 fish specimen), and in the southern part of the ocean (on 18 fish specimens).

I have already studied a great part of the Indian Ocean collection (consisting of Dubina's, Tkachuk's, and Gitchenok's collections). Thirty-five didymozoida species are recorded—60% of them new. Besides the collections taken near the Australian coast, in the Greater Australian Bay region, in the Red Sea, in Aden Bay,

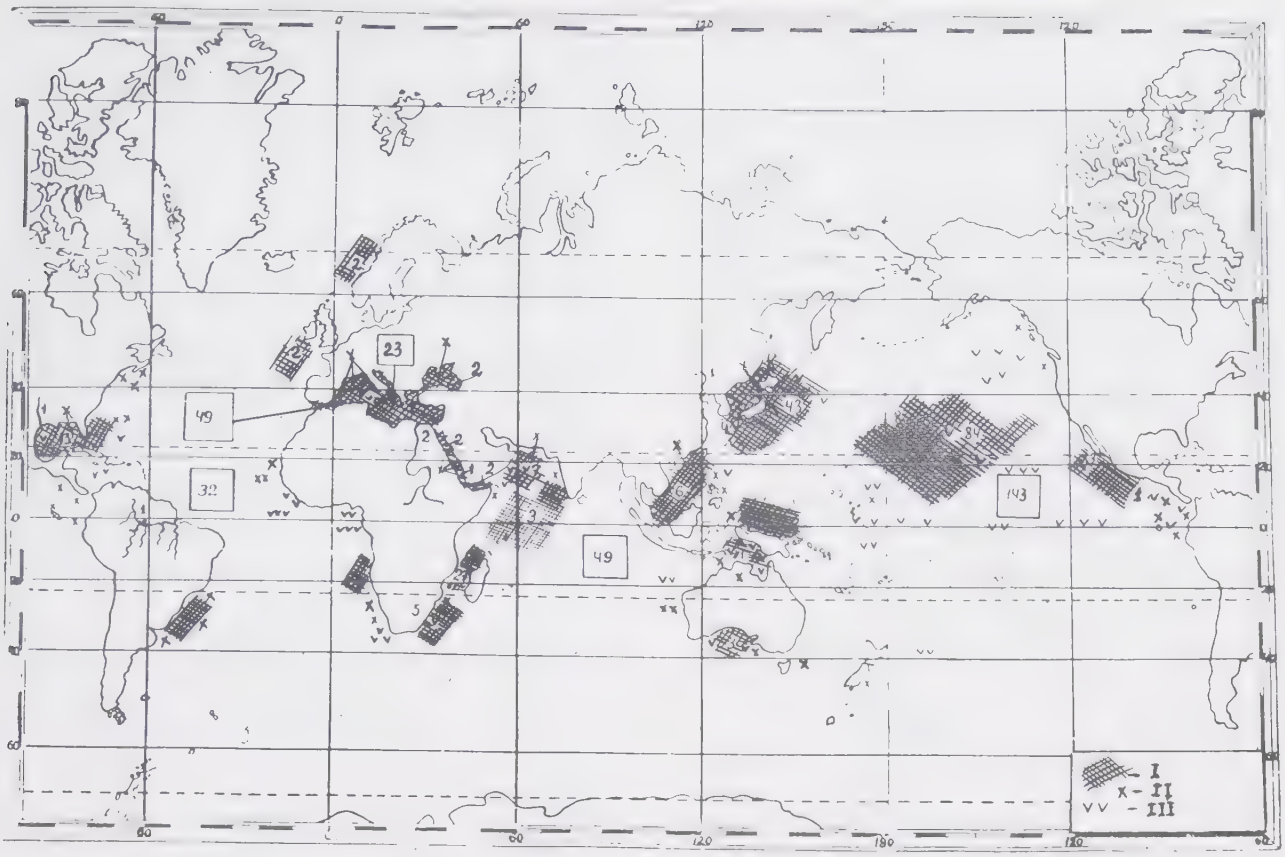

Figure 4.—Geographic distribution of didymozoids. I = Distribution of separate species; II = distribution of metacercariae; III = regions where didymozoids have been collected.

and in the Arabian Sea near the southeast coast of Africa being at my disposal; I have also the Atlantic Ocean collections, taken both in a special tunny [tuna] catching expedition (Nikolaeva's and Shchepkina's collections) and during full parasitological examination of other fishes. There are didymozoids collected in the tropical waters of the Guinean Bay in the region of Cape Blanc and Wallfish Bay. In the Northern Hemisphere, didymozoids have been collected in the Caribbean Sea, the Gulf of Mexico, around Gibraltar, and in the Mediterranean Sea.

Thus, the didymozoida fauna of the World Ocean is chiefly tropical and subtropical. Only a few species have penetrated into the boreal and notal regions. There are no didymozoida [recorded] in the Arctic and Antarctic waters. Undoubtedly, the didymozoida fauna of the Pacific Ocean is the richest and the most diverse. Probably, the didymozoida originated in one of the regions [mentioned] here.

A number of species of this family are circumtropical but others are endemics. The settling of didymozoida maritae occurs mainly in their final hosts. However, transference with the intermediate and reservoir hosts is possible as well. The considerable variability in distribution and dynamics of a number of didymozoida is reflected on the borders of the range of these trematodes. Such variations are noted in the Black Sea. In 1950 to 1960 and before, two species of didymozoida, *Unitubulotestis pelamydis* from *Sarda sarda* and *Nematobothrium scombri* from *Scomber scombrus*, had been registered there. *Sarda sarda* is a constant inhabitant of the Black Sea. Lately its catch has been sharply reduced and the stock has not been taken by the fishery. *Scomber scombrus* usually migrates to the Black Sea, but since 10 yr ago it has disappeared from catches after fattening [after the feeding period ends]. It is known that the metacercariae of two species of didymozoida invade sprats and, rarely, nine species of other Black Sea fishes. The invasion of small pelagic fishes by metacercariae has been reduced following the reduction in numbers of one final host (*Sarda sarda*) and disappearance of the other (*Scomber scombrus*). So, in 1959 to 1961 sprat were infected (in the Danube region) up to 93.5% with an intensity of invasion of from 1 to 116 specimens per fish. In 1977 extensiveness [prevalence] was 1% and intensity of invasion [infection] was one metacercaria per fish.

More than 100 fish species of 32 families are recorded as hosts of didymozoida maritae. First of all they are representatives of the family Scombridae (18 species), Exocoetidae and Serranidae (11 species), Sphyraenidae (7 species), and Istiophoridae and Carangidae (6 species). The same host may have several species of didymozoid parasites. Thus, 37 didymozoida species are registered from *Thunnus albacares* in different regions of the World Ocean. *Katsuwonus pelamis* has 33 species of didymozoida, *Thunnus obesus*—25, *T. thynnus*—19; *T. alalunga*—16; *Euthunnus affinis*—14; *Scomber japonicus*—11; *Auxis thazard*—9; *Seriola quinqueradiata*—7; and *Makaira nigricans*—6 species of didymozoida. The fishes, which are the hosts of many species of these trematodes, live near the coast in the surface layers of the ocean and are pelagic at all stages of their life cycles. The appended list[4] shows that tunnies [tunas] and other representatives of this

[4]No host list was supplied with the manuscript by the author.

family are the preferred hosts. Seven of 15 genera of the family Scombridae are hosts of didymozoida. One hundred and thirty-six species of didymozoida (or 64.7%) are recorded from Scombridae.

A number of the didymozoid parasites of various species of tunny are of the same genera and species. Such taxonomic proximity of didymozoida species of tunnies of the World Ocean may be explained, except for the genetic relations, by area combination [overlapping ranges], the presence of cosmopolitan species, and by the high speed and long migrations of these fishes. All of these factors create conditions for invasion by the same helminths.

The common nature of the hosts' ecology and the same food spectrum confirmed this resemblance [commonality or close correlation]. The species composition and number of didymozoida species in each species of tunny have their peculiarities. They differ in the extensiveness [prevalence] and intensity of invasion [infection]. As a rule the tunnies, marlins, and scombrids are invaded [infected] by varous didymozoid species. Specificity of this trematode group is expressed at the genus level. Representatives of the genera *Colocyntotrema*, *Metadidymozoon*, *Neodidymozoon*, *Makairatrema*, and *Glomeritrema* are characteristic for marlins. These genera are not recorded from tunnies but many others are.

A great number of host species (64) have only one didymozoid species recorded. Fifteen species have two didymozoid species and four host species have four species each.

The utilization of a number of host species by didymozoida is very high. *Thunnus albacares* in the Gulf of Mexico is 100% infected. The invasion [infection] intensiveness is from 8 to 1,167 specimens (Nikolaeva 1968). In the Gulf of Guinea and in the central Atlantic the same host is generally infected and the intensity of infection is up to 148 specimens (Shchepkina 1976). Essentially, the figures on the intensity of infection should be doubled, since a great number of didymozoida is encysted and every cyst includes two species [author probably meant specimens] of didymozoida. It is the same for *T. albacares* in the Indian and Pacific Oceans.

There are practically no tunas invaded by didymozoids. Therefore the borders of didymozoida and the tuna's distribution coincide.[5]

Compared with the morphogenesis of the didymozoid marita phase, the didymozoida metacercariae are very primitive. Kurochkin and Nikolaeva (1978) suggested a provisional system for didymozoida metacercariae. Using the presence or absence of an acetabulum sucker, a pharnyx, a stomach, and glandular cells in the region of bifurcation as generic characters, 11 genera were described in all (Fig. 5). Dimensions of metacercariae, their suckers, the distance between suckers, shape of the intestine branches and chambers, the ratio of body length to its width, and other characters were assigned species importance.

Unfortunately, the complete life cycle of didymozoids is not known. The scheme for the cycle as proposed by me (Nikolaeva 1965) has been mostly accepted by Yamaguchi (1975) and other investigators. The first stages of the cycle are the least known. There is no new information about the parthenogenetic periods of the development of didymozoids, but my knowledge of the hosts of the metacercariae has been widened considerably. The metacercariae which invade small pelagic fishes have been known for some time. The list of these fishes has been considerably expanded.

[5]The meaning of this paragraph is somewhat obscure. It is presented as it was in the original manuscript. It would make better sense if the first sentence of the paragraph was eliminated.

Metacercariae are capable of numerous passages and acclimatization to unusual animals. This was confirmed when metacercariae were found even in the dogshark, *Squalus acanthias*. Recently, a considerable didymozoida metacercaria invasion was recorded from squids (a number of the works of Gaevskaya, Naidenova, and Nigmatullin) and on crustaceans (Reimer 1971). They have even been found free in plankton tests [samples] (Slankis and Schevchenko 1974).

The cycles of didymozoida development have been analyzed according to the scheme of the trophic relationships of the pelagic fishes in tropical waters of the World Ocean (Parin 1968). The cycles of didymozoida development proved to be complicated and varied [Fig. 6]. Didymozoida of flyingfishes of the genus *Gonapodasmius* have the shortest life cycles. Three hosts (molluscs, copepods, and fishes) take part in their life cycle and a postcyclic host is possible also. It may be a tunny [tuna] or other predatory fish. Postcyclic hosts for the genus *Gonapodasmius* could be human as well. The didymozoida parasites of the moonfish possess this type of development also. Incidentally, they are the longest worms of all the trematodes. *Nematobibothrioides histodii* reaches 12 m in length.

The development [life] cycles of didymozoids invading tunnies acutally include reservoir hosts. Such species of didymozoids [with reservoir hosts] are numerous. The role of reservoir hosts is borne by lanternfish, sprats, flyingfishes, and other small pelagic fishes and squids. Similar are the life cycles of didymozoids from marlins. Postcyclic hosts may take part in these cycles also. They may be sharks. It should be emphasized that the presence of postcyclic hosts is of greater importance than is believed.

As is known, all attempts to extract live miracidia from eggs have failed. First of all it is connected with the fact that most didymozoids (there are viviparous species) have an unformed miracidium in their eggs. For its further development it must get into a postcyclic host.

The people of tropical and subtropical countries customarily eat raw fish with spices. Such dishes are prepared from tunnies, marlins, flyingfishes, etc. Along with other helminths, didymozoids may be gotten [ingested] by people. In cases where maritae are ingested, people display transit eggs of didymozoids. This situation is known for the eggs of *Gonapodasmius* from flyingfishes in Japan (Kamegai 1971). However, these fishes may have didymozoid metacercariae which may be acclimatized to human bowels and begin the migrations peculiar to these larvae. It may be dangerous for humans.

In conclusion, it should be emphasized that experiments on the development [life] cycle of didymozoids (or its separate phases) are necessary for solution of many questions of the biology, morphology, and systematics of this trematode group. Investigation of this interesting group provides new aspects of information about their hosts, which are valuable [economically and ecologically] fishes.

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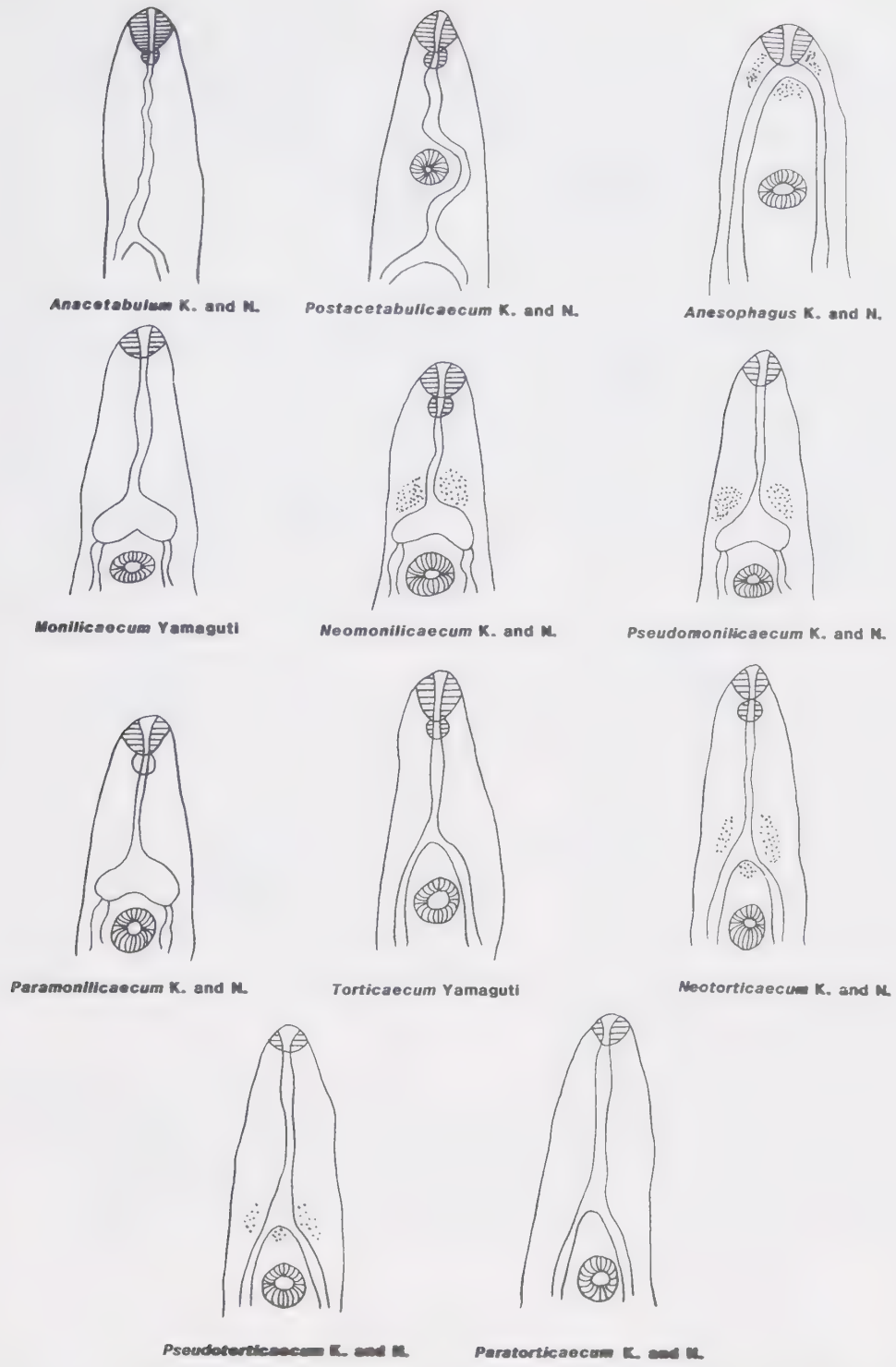

Figure 5.—Scheme of structure of anterior parts of didymozoid metacercaria (see Kurochkin and Nikolaeva 1978). [Those genera accompanied by the notation K. and N. were described in 1978 by Kurochkin and Nikolaeva.]

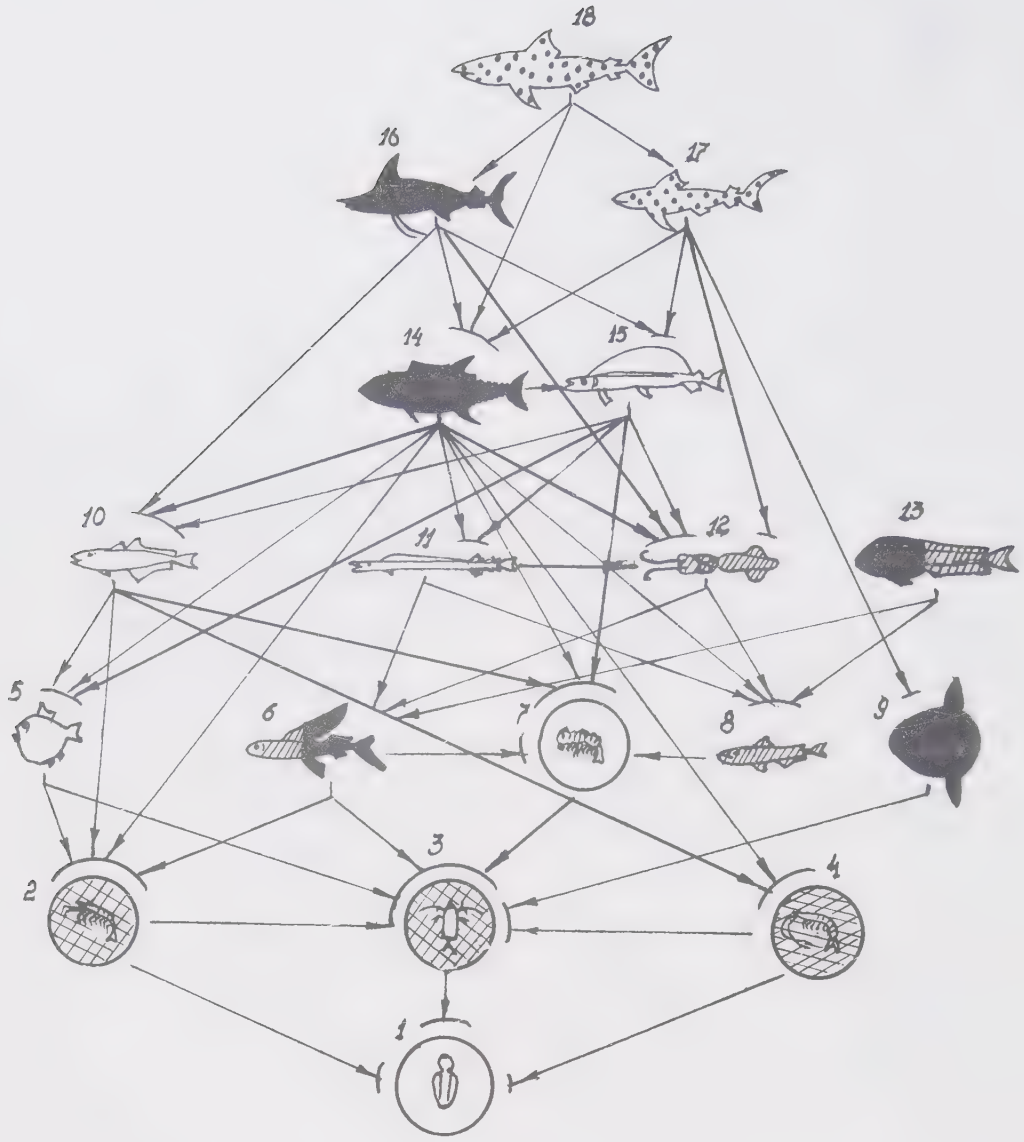

Figure 6.—Comparison of the cycle of didymozoid development to the scheme of trophic relationships of pelagic fishes. Intermediate hosts (cross-hatched) = Euphausiida (2), Copepoda (3), shrimps (4); reservoir hosts (hatched) = flyingfishes (6), lanternfish (8), squids (12), *Coryphaena* (13); definitive hosts (solid) = flyingfishes (6), sunfishes (9), *Coryphaena* (13), tuna (14), marlin (16); postcyclic hosts (dotted) = middle size shark (17), large shark (18); while not registered in cycle development didymozoid [those elements not recorded as taking part in the developmental cycle of didymozoids] (open) = fishes "of migrated layers" (5), hyperiida (7), small deep-water ichthyophages (10), gyvatina mackerel (11), alepisaurans (15); phytoplankton (1) do not take part.

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Comparative Analysis of Monogenean Faunas and Populations From Several Beloniformes Fishes[1]

L. A. GHICHENOK[2]

The material on which this paper is based, consists of a collection of monogeneans from 1,520 specimens of fishes belonging to 6 species of the garfish order, i.e., *Exocoetus volitans* and *E. monocirrhus* (Exocoetidae); *Euleptorhamphus viridis*, *Oxyporhamphus c. convexus* and *O. m. micropterus* (Hemirhamphidae); and *Cololabis saira* (Scomberesocidae). The majority of these fishes are component parts of the community of the oceanic epipelagic domain. Four of them (*E. volitans*, *E. monocirrhus*, *O. m. micropterus*, and *C. saira*) belong to the oceanic group proper, being permanent dwellers of the epipelagic domain. Though it can be found far away from the coast, *E. viridis* is a pseudo-oceanic species since it spawns in the neritic zone (Parin 1968). Only *O. c. convexus*, strongly related to coastal waters, belongs to the neritic group.

In all, 15 species and forms of monogeneans were recorded during this study, and all, except *Axine belones* from *E. volitans*, are recorded from the investigated fishes for the first time. Five monogenean species proved to be new, three representing new genera. No monogeneans were found in the saury.

A comparative analysis was conducted of both fauna and population of monogeneans from the fish species under study using quantitative measures of similarity. Following Beklemishev (1970), I describe as a fauna of some unit [of a particular portion] of the environment a complete list of animal species living there, while a population is a real comity of animals to be found there, which depends not only on the list of species to be found there, but also on the numbers of single-species populations.

The similarity of the monogenean fauna of single fish species was estimated by the well-known index of Jaccard (1912), the similarity of population, by the index $\frac{\Sigma a}{b+c-\Sigma a} \cdot 100\%$ where a is the least (of the two) index of abundance of each species common to both of the hosts being compared, while b and c are indices of abundance of all the species in or on hosts I and II, respectively.

An analysis of indices allows me to conclude that the similarity of monogenean faunas of individual fish species depends first of all on the amount of affinity [genetic or systematic] between the hosts. The closer the affinity, the greater the similarity of the species of one genus (0.56 and 0.57), the lowest, in fishes of different families (0.20).

The similarity of monogenean faunas seems to depend also on the ecological similarity of the hosts, but to a lesser degree. As a rule, fishes of the same ecological group have higher indices of similarity (0.30, 0.56, and 0.50). Nevertheless the index of similarity between the most ecologically different oceanic and neritic groups is far from being the lowest (0.33).

According to my data, the most closely related fish species have the lowest indices of similarity of monogenean populations (18.3% and 5.4%); different genera of one family, 32%; and different fish families, 23%. Fishes of one ecological group have relatively high indices of similiarity of monogenean populations (14.7, 18.3, and 73%). The lowest index (7.6%) was recorded for the most ecologically different oceanic and neritic groups of fish.

This allows me to conclude that the similarity of the monogenean populations, in contrast to the similarity of species composition [faunas], does not show any clear dependence on the [systematic] affinities of the hosts, but chiefly depends on their ecological similarity.

[1]No Literature Cited section was supplied by the author.

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New Data on the Capsalid Fauna of the World Ocean and Questions of its Specificity[1]

T. P. EGOROVA[2]

Extensive materials on capsalids of the different regions of the Pacific, Indian, and South Atlantic Oceans and the Sea of Japan have been studied for the past 10 yr. Eighteen species of capsalids were recorded as a result of my study of the monogenean collections from 25 fish species.

1. *Capsala gotoi* Yamaguti, 1968 (from *Thunnus obesus*)
2. *C. martinierei* Bosc, 1811 (from *Mola mola*)
3. *C. neothunni* Yamaguti, 1968 (from *Thunnus albacares*)
4. *C. nozawae* (Goto, 1894) (from *Thunnus obesus*)
5. *C. ovalis* (Goto, 1894) (from *Istiophorus orientalis* and *Makaira ampla*)
6. *Capsaloides cristatus* Yamaguti, 1968 (from *Tetrapturus angustirostris*)
7. *C. magnaspinosus* Price, 1939 (from *Tetrapturus audax*)
8. *Tristoma coccineum* (Cuvier, 1817) (from *Xiphias gladius*)
9. *T. integrum* (Diesing, 1850)
10. *Nasicola klawei* (Stunkard, 1962) (from *Thunnus albacares*)
11. *Benedenia derzhavini* (Layman, 1930) (from *Sebastodes*[3] *glaucus*, *S. steindachheri*, *S. iracundus*, *Sebastodes intronigер*[3], *S. alutus*, *Helicolenus papillosus*, and Scorpaenidae g. et sp.)
12. *Entobdella hippoglossi* (Müller, 1776) (from *Reinchardtius hippoglossoides matsuurae*)
13. *E. squamula* (Heath, 1902) (from *Reinchardtius matsuurae* and *Sebastes glaucus*)
14. *Pseudobenedenia nototheniae* Johnston, 1931 (from *Notothenia rossi* and *N. macrocephala*)
15. *P. ovalis* Yamaguti, 1968 (from *Priacanthus boops* and *Sebastodes proriger*)
16. *Pseudoentobdella pugetensis* Robinson, 1961 (from *Atheresthes stomias*)
17. *Allosprostonia tauvinae* Lawler and Hargis, 1968 (from *Epinephelus orientalis* and *Decapterus punctatissimus*)
18. *Trochopus australis* Robinson, 1961 (from *Helicolenus papillosus*)

[1]No Literature Cited section was supplied by the author.

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[3]Though the author presented the generic name *Sebastodes* twice, the first one probably should have been *Sebastes*. Thus the first three species would belong in this genus. The citation of *Sebastes glaucus* as a host of *Entobdella squamula* tends to confirm this.

The family Capsalidae Baird, 1853 is presently divided into 177 species, 33 genera, and 7 subfamilies (according to Yamaguti 1963—113, 21, and 5, respectively).

My observations of the occurrence of genera on hosts revealed that of 33 known genera, 19 are restricted to a single fish family. Fifteen of them are monotypical. The other four genera, containing more than one species (*Ancyrocotyle*—2, *Dioncopseudobenedenia*—2, *Nitzschia*—3, and *Capsaloides*—8) are closely specific for fish of one specific family. Thus, Monogenea of the genus *Capsaloides* are only observed on the genera *Tetrapturus*, *Makaira*, and *Istiophorus* of the family Istiophoridae.

Monogenea of six genera (*Benedeniella*, *Pseudoentobdella*, *Metabenedeniella*, *Allobenedenia*, *Pseudallobenedenia*, and *Mediavaginia*) parasitize fish of two families. For example, the genus *Benedeniella* is recorded on members of the families Rhinopteridae (order Rajiformes) and Carangidae (order Perciformes), and the genus *Pseudoentobdella* is recorded on Aetobatidae (order Rajiformes) and Hippoglossidae (order Pleuronectiformes), i.e., on families not closely related, but the contrary is the case with the other four genera.

Members of the genera *Trochopus* and *Tristoma* are observed on eight families. The first occurs only on Perciformes, but the data of the second are questionable (according to Bychovski 1957). The genera *Entobdella*, *Megalocotyle*, and *Neobenedenia* are recorded on nine fish families. *Entobdella* parasitizes Pleuronectiformes and Rajiformes. Perciformes are typical for *Megalocotyle* and most species of *Neobenedenia*. Representatives of the genus *Capsala*, observed on 11 families, are also typical for fish of the order Perciformes. The genus *Encotyllabe* parasitizes 16 families of Perciformes (and possibly on Salmonidae).

Thirty-four fish families, mostly Perciformes (23 families in nature and 11 under artificial conditions), are recorded as hosts for Monogenea of the genus *Benedenia*.

Thus, capsalids parasitize Perciformes mainly (with the exception of the genus *Entobdella*, the species of which are mostly recorded on Pleuronectiformes and Rajiformes). These basic regularities are also reflected in our data. Of 10 fish families observed to have capsalids, 8 are related to the order Perciformes. Perciformes are confirmed as the primary hosts for capsalid monogeneans.

On the Taxonomic Position of the Monogenean, *Pseudaxine mexicana* Meserve, 1938

B. Iv. LEBEDEV[1]

In 1938 F. G. Meserve published a large list of fish monogeneans from the waters of the Galapagos Archipelago based on studies of the Allan Hancock Pacific Expedition collections. *Pseudaxine mexicana* Meserve, 1938 from the [Spanish] mackerel, *Scomberomorus maculatus* (Mitchill), of Tangola-Tangola (Mexico) was described in that paper along with other species.

In 1955, K. Koratha described a new species, *Pseudaxine texana*, from the same Spanish mackerel host species of the Caribbean Sea (Port Aransas) [Gulf of Mexico]. In 1956, W. J. Hargis, Jr. opined that these monogeneans are identical, and that the name *P. texana* Koratha, 1955 is a junior synonym of the name *P. mexicana* Meserve, 1938. Judging from the works of Hargis (1956), Yamaguti (1963), and some other authors, they are certainly related to the genus *Pseudaxine* Parona and Perugia, 1890.

My last revision of the genera *Pseudaxine* and *Pseudaxinoides* Lebedev, 1968 (see Lebedev 1977) led me to doubt the generic identification of the monogenean species described by F. Meserve and later mentioned by the other authors.

First, it is known (Yamaguti 1963; Dillon and Hargis 1965; Lebedev 1972, 1977; and others) that parasitism of carangid fishes (family Carangidae) is typical for species of the genus *Pseudaxine*; whereas *P. mexicana* is recorded only from mackerels of the family Cybiidae. *Pseudaxine indicana* Chauhan, 1945, described from sparid fishes (?)—family Sparidae, and not recorded since by anybody—is an exception. However, this one is a species dubia (Lebedev 1977).

Second, while analyzing the figure presented in the original description (Meserve 1938, fig. 9/60-63) I discovered that the clamps of *P. mexicana* have nothing in common with those of the other *Pseudaxine* spp. The external appearances of *P. mexicana* clamps are very similar to the clamps of the genus *Pricea* Chauhan, 1945 and less [similar] to those of the genus *Neothoracocotyle* Hargis, 1956. The clamps of *P. mexicana* have similar riblike thickenings in the lateral fields of the capsule and the same "barrel-like" shape of the anterior part of the mediobasal (main) spring. Additionally, other structures observed in the figure show that the clamps of *P. mexicana* resemble those of *Pricea* spp. (or *Neothoracocotyla* spp.) closely.

Third, and last, the type and form of the haptor, described and figured by F. Meserve, is perhaps [probably] typical for *Pricea*.

There is no doubt that *Pseudaxine mexicana* Meserve, 1938 has to be removed from the genus *Pseudaxine*. The question of its generic position (*Pricea* or another genus) can be decided only after exacting and careful reinvestigation of the type materials. Evidently, this mistake, having existed for more than 40 yr, must be corrected.

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Plerocercoids of Some Cestoda as Bioindicators of the Population Structure of *Podonema longipes*

G. V. AVDEEV[1]

ABSTRACT

Podonema longipes is an important commercial fish inhabiting the northwestern Pacific. During parasitological investigations of *P. longipes* I attempted to use some parasites as bioindicators to uncover certain features of its biology. The most suitable species were two plerocercoids (*Nybelinia* sp. and a diphyllobothriid larva) which have vividly expressed differences in invasion [infection] in comparison with other discovered [known] parasites. They are able to accumulate in a host during its entire life. A total of 267 individual fish of ages from 6 to 26 yr, caught off the Japanese and northern Kuril Islands in 1976-80, were studied. The level of infection by both species in the areas investigated is different. Infection by *Nybelinia* is higher off Japan. On the contrary, infection by diphyllobothriid larvae is higher in the area off the northern Kuril Islands.

Invasion of *P. longipes* by both species in the areas under comparison begins in different age groups. Around Japan infection by *Nybelinia* begins at ages from 9 to 11 yr and diphyllobothriid larvae at 12 to 14 yr; around the northern Kurils at 15 to 17 and 9 to 11 yr, respectively. Invasion by both species increases as the fish host ages.

Observed differences in infection of females and males by *Nybelinia* are the result of the different vertical distribution of older age groups of male and female *P. longipes* (i.e., increase of the relative number of males toward the upper limit of the habitat of *P. longipes* and, conversely, an increase of the relative number of females to the lower limit). The probability of infection by *Nybelinia* decreases as the habitat depth increases. This is confirmed by the higher infection by this parasite of Alaska pollock inhabiting the study area at lesser [shallower] depths.

Differences in the invasion by *Nybelinia* of males and females off the northern Kurils occur simultaneously with the beginning of infection by this parasite. In comparison in the area off Japan, differences in the infection of females and males are seen from the age groups of from 12 to 14 yr, while the beginning of infection takes place at 9 to 11 yr.

In the northern Kurils sex differentiation by depths of *P. longipes* begins in age groups of 15 to 17 yr, and off Japan 12 to 14 yr. Thus, the formation of differences in the infection of females and males by *Nybelinia* coincides with the beginning of sex differentiation by depth in each area.

My data reveal differences in the growth rates of males and females in older age groups. Besides, in the area of the northern Kurils, females begin to grow faster than males at the age of 18 and those off Japan, at the age of 12. As we see, in each of the areas mentioned, the age at which differences in growth rate between males and females begins coincides with the formation of differences in the infection of males and females by *Nybelinia* and [of] differential sex distribution by depth.

Thus, it may be assumed that in each of the areas investigated an independent *P. longipes* population, having its specific parasitological and biological characteristics, exists.

In recent years the practice of using parasitological data to study the ecology of commercial species has become of great importance. The use of parasites as biological tags has permitted the study of population structure and migrations of certain species (Baudin-Laurencin 1971; Margolis 1963; Kabata 1963; Kovaliova 1965; Konovalov 1971; Kabata and Forrester 1974; Platt 1976; and others).

During parasitological studies of *P. longipes* I succeeded in using certain parasites as bioindicators in order to reveal some features of the biology of this fish. The most suitable [parasites for this purpose] turned out to be the plerocercoids of two species: A *Nybelinia* sp. and a diphyllobothriid larva. In comparison with other parasites found on *P. longipes*, their invasion level [infection level[2]] has most vividly demonstrated differences related to a number of factors (i.e., fishing ground, depth of residence, age, and sex of the host). Further, both plerocercoids can be accumulated in *P. longipes* during its entire life.

Altogether 2,671 fishes of ages from 6 to 26 yr caught off Japan and around the northern Kuril Isles during 1976-80 were studied.

Analysis of the invasion level of *P. longipes* by these two parasite species permitted discovery of the following specific features:

1) The invasion [infection] level by the plerocercoids of both species in the [geographical] areas under investigation is different. Extensity [prevalence] and intensity of invasion [infection] by *Nybelinia* larvae is higher around Japan. Conversely, invasion by diphyllobothriid larvae is much higher in the waters around the northern Kuril Islands (see Table 1).

2) The extensity [prevalence] and mean intensity of invasion [infection] by *Nybelinia* larvae increase as the fish age. In older age groups (i.e., more than 20 yr of age), the rate of increase of invasion in the area of the northern Kuril Isles lowers [is reduced]; in the area of Japan, invasion [infection] actually decreases (Fig. 1 A, B). Invasion by diphyllobothriid larvae in both areas becomes higher with advancing age of the fish (Fig. 1 C, D).

3) The level of invasion of host males by *Nybelinia* larvae is higher than of females in both areas (Fig. 2). As for diphyllobothriid larvae, male hosts have a higher level of invasion [infection]

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[2]In this as well as other papers in this volume, the word invasion means infection, usually, and can be used in its place.

Table 1.—Mean intensities of parasite infestation with location.

Depth (m)	Number of fish studied	*Nybelinia surmenicola* %	*Nybelinia surmenicola* mean intensity	Diphyllobothriidae g. sp. %	Diphyllobothriidae g. sp. mean intensity
		Northern Kuril Isles			
200-570	401	42.3	2.4	50.0	2.5
580-710	656	36.7	1.7	51.7	2.7
730-1,120	501	16.9	0.6	34.1	1.3
200-1,120	1,558	31.8	1.5	45.9	2.2
		Japan			
210-540	397	70.3	8.7	24.4	0.6
550-700	383	68.9	6.2	32.3	1.0
710-930	333	81.7	4.1	54.6	1.9
210-930	1,113	75.2	6.5	35.7	1.1

in the area of the northern Kuril Isles, with the females being invaded more heavily around Japan (Fig. 3).

4) In both areas a decrease of invasion by *Nybelinia* larvae takes place as the depth at which the host lives or was captured increases (see Table 1). Invasion by diphyllobothriid larvae lowers [decreases] as the depth lowers [increases] in the area of the northern Kuril Isles [generally speaking[3]] and increases around Japan.

Below I shall attempt to explain the above-mentioned specific features of the invasion of *P. longipes* by Cestoda larvae (Table 1).

The unequal invasion of *P. longipes* by larvae of both *Nybelinia* and diphyllobothriidae in the areas being compared is caused by the different possibility of [opportunities for] invasion of the hosts by these parasites in each area. Obviously this occurs because of the greater abundance of the procercoids of *Nybelinia* in the planktonic crustaceans constituting the diet of *P. longipes* around Japan and the reduced abundance of the procercoids of diphyllobothriidae in the area of the northern Kuril Isles. At that, a higher concentration of crustaceans (the intermediate hosts) in the total plankton biomass in this area is possible, as well as a higher occurrence of procercoids on the intermediate hosts, themselves, as well as the high abundance of mackerel sharks, which are the final hosts of *Nybelinia* in this area according to the data of ichthyologists. I should note that invasion by *Nybelinia* from north to

[3]The phrase "generally speaking" in brackets is employed because in Table 1 the percentage of fish invaded and the intensity of invasion by *Diphyllobothrium* are actually slightly higher at mid-depths in the northern Kurils than at the surface. However, at greater depths both parameters are much lower!

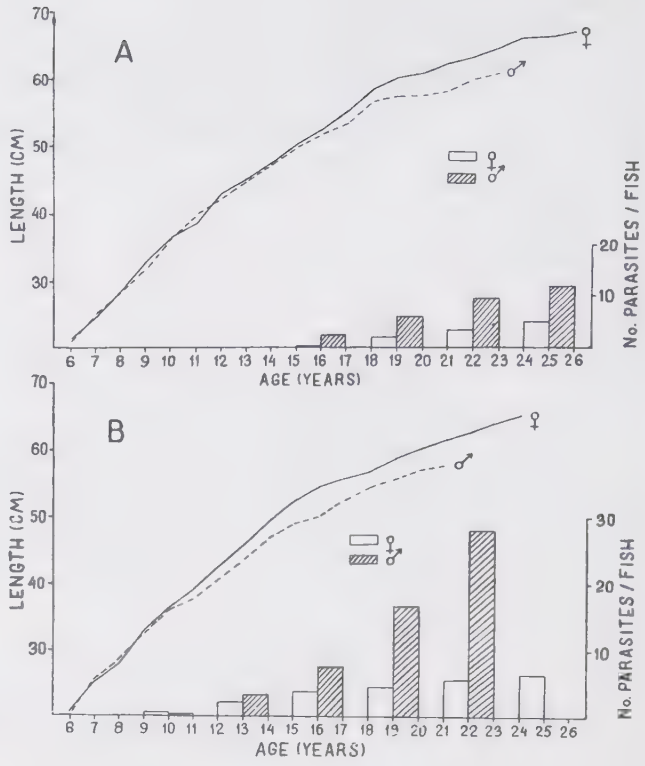

Figure 2.—Average intensity of infestation [infection] with Nybeliniae and the average body length of males and females of *Podonema longipes* depending on fish age: A = North Kuril Islands waters; B = Japan Islands waters.

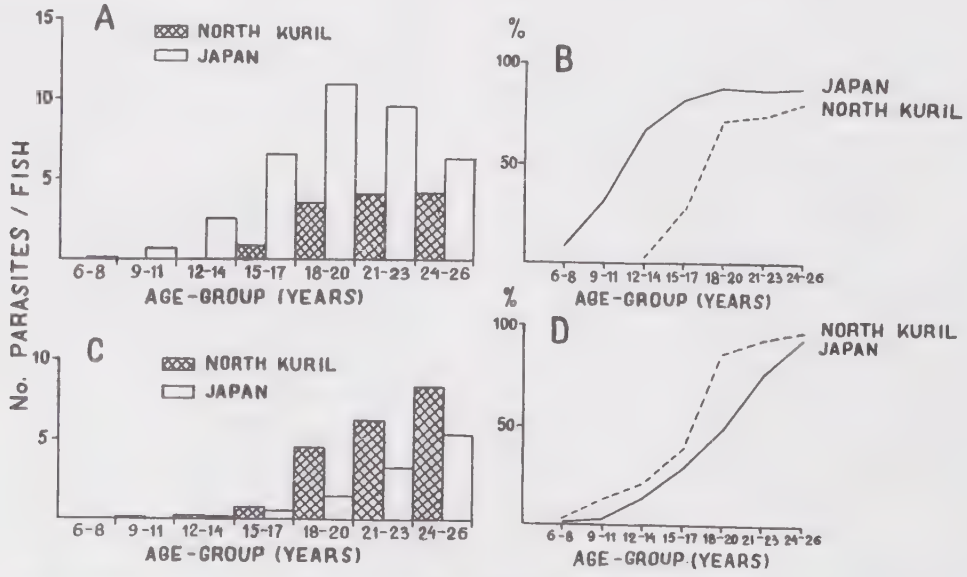

Figure 1.—Percent occurrence and average intensity of infestation [infection] of *Podonema longipes* with cestode plerocercoids depending on fish age: A, B = *Nybelinia surmenicola*; C, D = Diphyllobothriidae.

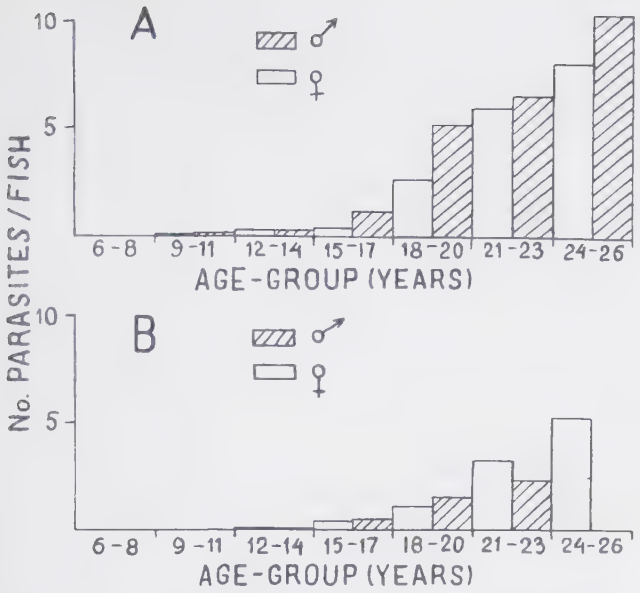

Figure 3.—Average intensity of infestation [infection] with diphyllobothriid larvae of males and females of *Podonema longipes* depending on fish age: A = North Kuril Islands waters; B= Japan Islands waters.

south has been observed on Alaska pollock as well (Mamaev et al. 1965). This obviously involves other fish species also.

The increase of invasion [infection] as *P. longipes* grows older is caused by the ability of the larvae to live in the body of the host during the latter's entire life. I have never observed dead plerocercoids in *P. longipes*.

I already know from the literature (Mamaev et al. 1965) the opinion of those authors that, in the Bering Sea and the Gulf of Alaska, the greater the depth of residence of Alaska pollock the lower the invasion [infection] by *Nybelinia* larvae. In the case of Alaska pollock, as well as of *P. longipes*, the possibility of invasion by *Nybelinia* larvae apparently is reduced as the depth of their residence increases. The differing invasion [infection] of *P. longipes* and Alaska pollock in the area under investigation confirms this. As I know, *P. longipes* and Alaska pollock are interchangeable [comparable or overlapping?] species in their distribution. Alaska pollock resides at lower [shallower] depths and, in comparison with *P. longipes*, is more heavily invaded [infected] by *Nybelinia* larvae.

In order to understand the reasons for the differing levels of invasion of male and female *P. longipes* by plerocercoids, I analyzed the sex ratio of *P. longipes* according to the depth of capture. It was found that the vertical distribution of male and female juveniles and older fish differs significantly. A relative increase of female abundance is observed in fish older than 14 yr in the area of the northern Kuril Isles and in fish older than 11 yr around Japan in the direction of the lower boundary of *P. longipes* residence [in respect to depth], and, on the contrary, the number of males increases as the depth lowers or decreases. The younger fish show no change in sex ratio with an increase in depth. Females residing in mainly higher [greater] depths are invaded by *Nybelinia* to a lower [lesser] extent and total invasion of *P. longipes* decreases with an increase in depth.

The fact that in each area the age at which a different vertical distribution of *P. longipes* sexes begins to appear, coincides with the age at which the difference in invasion [infection] by *Nybelinia* between males and females appears, proves the correctness of the above-stated explanation concerning the availability [causes] of the differences in invasion of *P. longipes*. The difference in invasion by *Nybelinia* larvae between the sexes of *P. longipes* in the area of the northern Kuril Isles appears simultaneously with the beginning of invasion (15 to 17 yr), and around Japan from the moment of the sharp increase in invasion (12 to 14 yr). However, the beginning of invasion by *Nybelinia* occurs at the age group of 9 to 11 yr.

As for the diphyllobothriid larvae of the northern Kuril Isles area, here I may discern a pattern close to that of *Nybelinia* larvae: Invasion decreases with increase of depth and males have a higher level of invasion than do females. Apparently, the possibility of invasion by diphyllobothriid larvae diminishes as the depth increases in this area.

In contrast, around Japan, invasion by diphyllobothriid larvae increases with depth and females have the higher level of invasion. This pattern of invasion is possible only in the case where the possibility of invasion by this parasite increases as the depth increases. Apparently this is the case for this area.

In the northern Kuril Isles, the age at which the differences in the invasion [infection] of males and females by diphyllobothriid larvae appear coincides with the sharp increase in invasion (15 to 17 yr), i.e., with the beginning of the change in vertical distribution of *P. longipes*. *Podonema longipes* individuals begin to be invaded in this area at the age of 9 to 11 yr. A similar distinct relationship was not observed around Japan.

Females of *P. longipes* older than 20 yr dominate at all depth ranges of their residence. Evidently males have a higher mortality level than females. As already mentioned, females are invaded by *Nybelinia* to a lesser extent, which is why the total invasion [infection] of older fishes decreases. A similar decrease in invasion by diphyllobothriid larvae does not occur, so a difference in invasion [infection] of males and females by this parasite is not so evident as is the case with *Nybelinia* larvae.

For a difference in invasion of males and females of *P. longipes* to reach the values observed, a prolonged time of existence of the different vertical distribution within the yearly cycle of *P. longipes* is necessary. Figure 4 (sexual distribution of *P. longipes*) shows that the pattern described above continues during the different seasons. I suppose that this vertical distribution of males and females is interrupted only during spawning, but have no data on this point. However, the spawning period is not very long, usually, and the intensity of feeding by the fish diminishes sharply at this period or ceases altogether.

By analyzing the data on age of *P. longipes* obtained during parasitological dissections of fishes, I managed to detect differences in the rate of growth of males and females in the mature age groups (Fig. 2). At that, females of the northern Kuril Isles begin to overtake males in growth at about 17 to 18 yr of age, while around Japan they do so at 11 to 12 yr of age.

As may be seen, in every area studied the age at which the difference in growth rate between males and females appears coincides with the inception of sexual differentiation by depth, as does the beginning of the differences in invasion of male and female hosts by *Nybelinia*. Around the northern Kuril Isles these features of *P. longipes* appear in the age group of 15 to 17 yr; around Japan, at the age of 12 to 14 yr. Apparently the simultaneous beginning of these phenomenona in *P. longipes* is connected with its attainment of sexual maturity, which begins in fishes of younger age in Japanese waters than in the fish of the northern Kuril Isles.

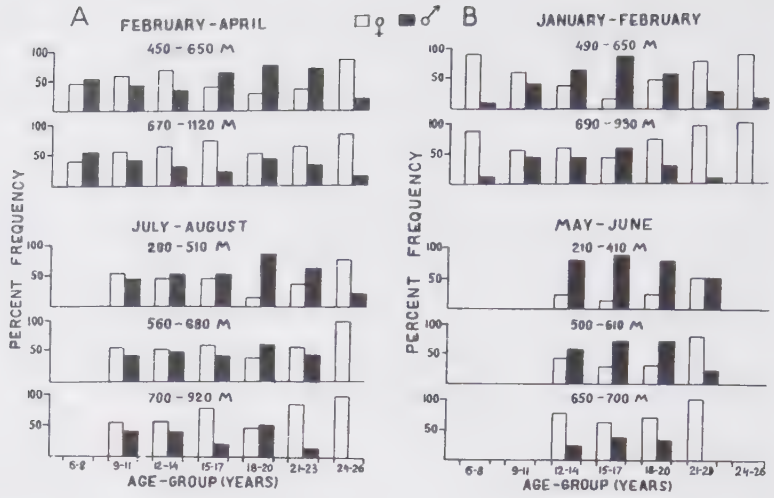

Figure 4.—Sex interrelations of *Podonema longipes* from different depths: A = North Kuril Islands waters; B = Japan Islands waters.

On the basis of the above, I may postulate that independent populations of *P. longipes* exist in every area of investigation and that each has its own parasitological and biological characteristics.

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Development of Larval Stages of *Bothriocephalus scorpii*

A. I. SOLONCHENKO[1]

ABSTRACT

I determined that the cycle of development of *Bothriocephalus scorpii* may proceed with either one intermediate host (Copepoda) or two (Copepoda and fish).

Bothriocephalus scorpii was found to infect *Scophthalmus maeoticus torosus* and *Sc. m. maeoticus* up to 100%, with an intensity of invasion [infection] of from 2 to 90 specimens. Even young individuals (3 cm in length) which had just been transformed were found by Bulgurkov (1963) to be infected by *B. scorpii*. Since plaice is the object of aquaculture, *B. scorpii* may represent an essential danger for their larvae and young specimens, causing bothriocephalus disease. To investigate this possibility was the objective of my studies of the life cycle of this cestode. According to the literature, development of *B. scorpii* involves the participation of one intermediate copepod host (Essex 1928) or the participation of two intermediate hosts, a copepod and a fish (Markovski 1935).

Markovski (1935) infected the copepod *Eurytemora hirrundo* with coracidia and examined them only on the 4th and the 17th days of development. The occurrence of calcifications, of cercomers, and the timing of their appearance as plerocercoids were not explained [discovered] by him due to the brevity of the experiment. He found the second intermediate host during autopsy of *Gobius minutus*. Feeding their intestines containing the plerocercoids he had found to gloss, he obtained a fully grown stage of the adult helminth.

I found plerocercoids of *B. scorpii* in *Trachurus mediterraneus ponticus* and *Odontogadus merlangus* in the Azov Sea and Naidenova (1974) found that *Gobius* had them too.

I determined the period of development and the emergence of the coracidium from the eggs as well as its viability under different temperature regimes (Solonchenko 1979). To discover the second intermediate host, I used the bottom fishes *Gobius minutus* and *Scorpaena porcus*. Like plaice, *S. porcus* is also a definitive host of *B. scorpii*. Five *Acartia clausi* containing procercoids were introduced by dropper [syringe] into the ventricles of two *Gobius minutus* and *Scorpaena porcus*. One *Scorpaena porcus* was dissected on the 6th day of development of *B. scorpii* and a contractile compressed body of rounded shape, with a size of 0.602 × 0.392 mm was found. The cuticula of the body was found to be smooth, containing many calciferous bodies of different shapes and sizes in the parenchyma. No bothrium was found at this time. Upon penetration into the body cavity of *Gobius minutus*, the procercoids lose the long appendage-bearing hook which is connected with the main part of the body by a narrow isthmus. On the 18th day of development, the bodies of the procercoids increased in size up to 0.938 × 0.431 mm (Fig. 1). The body of the procercoids in *Scorpaena porcus* had attained an elongated shape with a size of 0.602 × 0.126 mm by the 18th day of development. The anterior portion was expanded and one could clearly distinguish the formation of the scolex. The remainder of the body was of the same width, 0.098 mm. On both sides [of the body] there are slight transverse furrows, out of which the limbs [appendages?] are formed. The cuticula of the body is smooth and there are calcifications of different shapes and sizes in the parenchyma (Fig. 2).

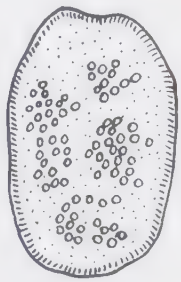

Figure 1.—Plerocercoid from *Gobius minutus* on the 18th day of development.

Unfortunately I could not follow the development of *B. scorpii* further. However, it has been clearly shown experimentally that plerocercoids can develop in both *Gobius minutus* and *Scorpaena porcus*. Development proceeds primarily in a different fashion in *Gobius minutus*, the second intermediate host in which only the scolex develops; while in *Scorpaena porcus*, the definitive host of *B. scorpii*, the parasite begins to develop the scolex and the strobilae simultaneously.

Thus, I have established that the cycle of development of *B. scorpii* may proceed with the participation of one intermediate host or with two. Plaice may be infected in two ways: 1) Through the copepod, when they feed on the plankton (the larval stage), or 2) through the fish (when they are eaten).

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Figure 2.—Plerocercoid from *Scorpaena porcus* on the 18th day of development.

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Special Features of the Geographical Distribution and Practical Significance of the Parasitic Copepods of Fishes of the Pacific[1]

V. N. KAZACHENKO[2] and V. M. TITAR[3]

ZOOGEOGRAPHICAL ASPECTS

At present, 1,700 species of copepods parasitizing fish, representing 256 genera, are known. About 1,450 species of 232 genera, i.e., 85.3% are sea [marine] species. Approximately 700 species of 173 genera of parasitic copepods of sea [marine] fishes were recorded in the Pacific Ocean. Thus, some 48% of all known sea [marine] parasitic copepods were found in the Pacific Ocean.

Parasitic copepods are distributed as are the hosts of those parasitic copepods (Kazachenko and Titar 1980). Second, as was found (Titar in litt.) in the case of *Pumiliopes capitulatus*, the distribution of parasitic copepods depends mainly on the distribution of water masses (after Dobrovolski 1961). And last, historical factors, primarily the geological history of the Pacific Ocean, paleoclimatological changes, etc., are of great importance, enabling us to solve such problems as amphiboreal distribution, bipolarity, etc.

The peculiarities [special features] of bottom geomorphology, vertical structure of water masses, and the presence of vast water spaces in the Pacific Ocean make possible the existence of several main complexes of parasitic copepods there, i.e., coastal (shelf), epipelagic, and deep water ones. On the whole these complexes correspond to those defined for sea fish (Parin 1968). As a rule, the special features of the geographical distribution of copepods from the various complexes are different. So, we shall consider them separately, beginning with the shelf fauna.

In all, 554 species of 125 genera of 25 families of parasitic copepods are recorded from shelf fishes of the Pacific Ocean. Analysis of this material has shown that all of the copepod families have many more tropical representatives (400) in their composition than boreal (97) or notal (48) ones. The representatives of the families Euryphoridae, Kroyeridae, Pseudocychidae, and Tegobomolochidae were recorded only from the tropical (together with the subtropical) part of the Pacific Ocean on shelf fishes. Many genera are also confined primarily to the tropics in distribution. For example, from the family Bomolochidae there were recorded *Nothobomolochus*, *Orbitacolax*, *Pumiliopes*, *Unicolax*, and *Pumilopsis*; from Caligidae, the genera *Anuretes*, *Caligulus*, *Dentigryps*, *Heniochophilus*, *Mappates*, *Parapetalus*, *Pseudanuretes*, *Pseudocaligus*, *Pseudopetalus*, *Pupulina*, *Sciaenophilus*, and *Synestius*; from the family Chondracanthidae, the genera *Brachiochondria*, *Ceratochondria*, *Humphreysia*, *Immanthe*, *Juanettia*, *Neobrachiochondria*, *Praecidochondria*, *Prochondracanthopsis*, *Prochondracanthus*, *Protochondria*, *Pseudacanthocanthopsis*, *Pseudoblias*, *Pseudodiocus*, and *Scheherazade*; from the family Eudactylinidae, the genera *Bariaka* and *Nemesis*; from the family Lernaeoceridae, the genera *Impexus* and *Peniculisa*; from the family Lernaeopodidae, the genera *Anaclavella*, *Clavellisa*, *Clavellopsis*, *Epiclavella*, *Isobranchia*, and *Thysanote*; from the family Lernanthropidae, the genera *Norion* and *Sagum*; from the family Pandaridae, the genera *Dinemoleus* and *Pseudopandarus*; from the family Philichthyidae, the genus *Ichthyotaces*; and from the family Taeniacanthidae, the genera *Anchistrotos*, *Metataeniacanthus*, *Parataeniacanthus*, *Pseudotaeniacanthus*, *Taeniacanthus*, and *Taeniastrotos*.

Most of the parasitic copepods of shelf fish of the tropical Pacific are distributed circumtropically. Representatives of the above genera (as well as circumtropical species) are rarely found beyond the tropical regions. Their appearance, for example, in Peter the Great Bay (the Sea of Japan) is caused by the heating of the subsurface layer in summer, forming water masses whose temperature characteristics are very close to those of the surface water masses of tropical seas.

The largest quantity of tropical parasitic copepod species of shelf fish was registered [recorded] in the western Pacific, which is part of the Indo-West Pacific region. For example, in the western Pacific, 334 tropical species were registered [recorded], but in the eastern Pacific only 60 were reported. It is rather difficult to understand the reasons for the extraordinary abundance of [species in] the Indo-West Pacific fauna. On the one hand, we may assume that a larger quantity of ecological niches (hosts) exists in the western Pacific and as a result of that, a larger quantity of parasitic copepod species. On the other hand, Ekman (1953), who studied the entire fauna, preferred to explain this by the fact that the present Indo-West Pacific fauna is in some ways a relict of the Tethys fauna; and the greater number of Tethys relicts belongs to the Indo-Malaysian archipelago. The assumption of Ekman is probably true with regard to the tropical fauna of parasitic copepods.

As was mentioned, the boreal and notal parasitic copepod species in the Pacific Ocean are fewer in quantity than tropical ones. [However] boreal and notal waters are inhabited by many copepods: i.e., from the family Caligidae, the genus *Pseudolepeophtheirus*; from the family Chondracanthidae, the genera *Diocus* and *Markevitchielinus*; from the family Lernaeoceridae, the genera *Haemobaphes* and *Trifur*; from the family Lernaeopodidae, the genera *Charopinus*, *Dendrapta*, *Lernaeopodina*, and *Nectobrachia*; from the family Lernanthropidae the genera *Aethon* and *Paraleranthropus*; and from the family Pandaridae the genus *Demoleus*.

The genera consisting of a large number of species such as *Acanthochondria*, *Chrondracanthus*, *Lepeophtheirus*, *Brachiella*, and others, have representatives in both tropical and boreal (notal) waters. Such distribution can be explained by the wide, adaptive radiation of these species, which extend also to the hosts of non-

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tropical areas of the Pacific Ocean and even of the other ecological zones (epipelagic, bathyal, etc.).

The complex of parasitic copepods second in number of species is the epipelagic. There were 119 species of 49 genera and 16 families registered in this complex. We have studied the distribution of parasitic copepods by ichthyogeographical areas as determined by Parin (1968) for the epipelagic zone. The southern boreal area is inhabited by 9 species of 6 genera; the northern subtropical area, by 77 species of 38 genera; the tropical area, by 76 species of 36 genera; and the southern subtropical, by 33 species of 21 genera. It is evident that the majority of species of the epipelagic complex inhabits tropical (subtropical) waters as is the case with the shelf fauna. It is noteworthy that the northern boreal area lacks a specific epipelagical ichthyofauna almost completely. This fauna has been ecologically substituted [replaced] in this area by fishes of the salmon genus, *Onchorhynchus*. The copepod *Lepeophtheirus salmonis*, being often found on these salmon, can be considered as almost the only representative of this group in the epipelagical zone of the northern boreal area.

The approximately equal numbers of species and genera of parasitic copepods recorded in northern subtropical and tropical areas is due to the better knowledge of the former area, i.e., the area of Japan. Approximately half the parasitic copepods were registered [recorded] in the southern subtropical area rather than in the tropical area, which is quite natural. The numbers of parasitic copepods in the southern subtropical (33) and notal (30) areas are also approximately equal. Many tropical species were registered in the latter area. Most were found near New Zealand. This type of distribution of parasitic copepod species suggests that the boundary between the northern subtropical and notal areas off the coast of New Zealand must extend further to the south. But the geographical distribution of parasitic copepods of epipelagic fish requires additional investigation.

The deep-water complex of parasitic copepods has been investigated even more poorly. The Pacific Ocean complex consists of 44 species of 26 genera of 9 families. The species of the deep-water complex generally belong to the same families as those species inhabiting the shelf (i.e., Lernaeoceridae, Lernaeopodidae, Sphyriidae, Chondracanthidae, etc.). The only exception is the family Hyponeoidae, consisting of a single species, *Hyponeo australis*, and found only in deep water.

Different groups of parasitic copepods must have moved into the ocean depths quite independently and at different times. This is confirmed by the diversity of taxonomic isolation of parasitic copepods of deep-water fish in comparison with those found on shelf fish: From various species of the same genus to the self-sustained family.[4] Therefore, deep-water species of parasitic copepods are divided into two groups—an ancient [or primarily] deep-water group and a secondary one (Titar 1979). Each of these groups has its own special features of geographical distribution. The ancient deep-water group is characterized, as a rule, by vast (most often panoceanic) areas of residence. For example, the area of residence of *Sarcotretes eristaliformis* covers the depths of the Pacific, Indian, and Atlantic Oceans. The stable environmental conditions of the vast deep-water masses probably contribute to such a wide distribution. On the contrary, the secondary deep-water species (the establishment of which took place quite recently in terms of geological time) have much more limited areas of residence. Many of them occur only in the northwestern portion of the Pacific Ocean.

[4]This phrase is presented as it was in the original manuscript.

It should be noted that some deep-water parasitic copepods (i.e., *Hyponeo australis* and *Periplexis antarcticensis*) might serve as an example of false bipolarity. The well-known phenomenon of isothermic submergence accounts satisfactorily for the distribution of such copepods (Ekman 1953).

PRACTICAL ASPECTS

We now proceed to a discussion of the practical significance of parasitic copepods. Since there are no monographs, except the book by Kabata (1976), on the practical significance of parasitic copepods, it is worthwhile to provide a general assessment of their significance according to the following aspects: 1) Influence of parasitic copepods on the hosts; 2) the role of parasitic copepods in ecosystems; 3) the significance of parasitic copepods for commercial fisheries; and 4) utilization of parasitic copepods for solving scientific and practical problems.

1) The influence of parasitic copepods on their hosts is established by their influence on organs, tissues, and on the organism of the host as a whole.

The influence of copepods is most often demonstrated by various changes in the quantitative characteristics of fish (weight, body length, and body proportions). Numerous works show that parasitic copepods reduce the weight of fish (Broek 1978; Grabda 1957; Nataraian and Balakrishnan 1977; and others). Losses in fish weight range from 3 to 50% (Abrosov et al. 1963; Dieuzeide and Roland 1956; Kabata 1958; Lechler 1935; Mann 1964) and muscles suffer the heaviest losses in comparison with other parts of the fish (Kabata 1970). The loss of weight is closely correlated with such characteristics as the coefficient of body condition, which decreases for infected fish (Abrosov et al. 1963; Pronin et al. 1975; Harding and Wheeler 1958; Hotta 1962; Reichenback-Klinke et al. 1968; Schaperclaus 1954). The proportions of the fish body also change; the heads of infected fish are relatively larger and the bodies are thinner than those of uninfected fish. The percentage of water content changes as well, increasing by 8% in contaminated [infected] fish (Debrosses 1948; Mann 1960; Kabata 1970). Total weight decrease is related to a reduction in fatness. Fat content is reduced two to four times in fish infected by copepods (Abrosov et al. 1963; Kabata 1958).

Infected areas in fish muscles [to be used for human food] must be removed because of copepods. For instance, *Panella hawaiiensis* infects from 2 to 5 cm^3 of the muscle tissue of boarfish, *Pentaceros richardsoni*, that is an average of 3% and a maximum of 16% of the muscles of the infected boarfish (Kazachenko and Kurochkin 1974). This *Penella* usually accumulates in the host's body throughout its entire life span. The same is true for the copepod *Sphyrion lumpi* infecting the redfish, *Sebastes mentella* and *Sebastes marinus*. Sphyrions can infect up to 90% of fish of commercial size at numbers up to seven parasites each (Berland 1969; Herrington et al. 1940; Kelly and Barker 1965; Nigrelli and Firth 1939; Perlmutter 1951; Templeman and Squires 1960; Williams 1963).

As is quoted in many works (Abrosov et al. 1963; Denisov 1977; Gjøsaeter 1971; Kelly and Barker 1965; Lechler 1935; Nataraian and Balakrishnan 1977), copepods affect the length [entirety] of the host's body. Gills are most often infected. Within the branchial system filaments, gill rakers, and gill arches are generally infected. Parasitic copepods cause hypertrophy of gill filaments and gill rakers (Kazachenko and Valova 1979) and mucus formation at the surface of gill filaments. Also fusion of the gill filaments takes place with the hypertrophy of gill epithelium

(Kabata and Cousens 1977; Khalifa and Post 1976). The branchial system is most infected by the genera *Haemobaphes* and *Lernaeocera*, although their invasion intensity is usually not high (Froiland 1974; Grabda 1975, 1977; Kabata 1958; Rojo 1959).

Parasitic copepods are able to damage fish skin while feeding on mucus, epidermis, and even blood of the host, forming skin sores and causing hyperemia, pigmentation, and necrosis (Baudouin 1917; Boxshall 1977; Dzidziul 1973; Grabda 1972; Shotter 1971). Copepods make fish skin thinner and may destroy it completely (Hotta 1962; Khalifa and Post 1976; Luling 1953; White 1940).

The parasites *Phrixocephalus cincinnatus* and *Colobomatus kyphosus* infect the sense organs of the fish. The first infects halibut's (*Atherestes stomias*) eyes causing complete blindness of the eyes and hematoma in the eyeball. The color of the eye becomes red and eye volume increases. Some 82.8% of halibut is infected by *Ph. cincinnatus*. Parasites are more often attached to the right eye (66%) than to the left one (5.7%); 28.3% of fish had both eyes infected, with the number of copepods larger in the right eye than the left (Kabata 1967, 1969; Kabata and Forrester 1974). Fish eyes are often affected by copepods of the genus *Lernaeenicus* with a resultant loss of sight (Carvalho 1953; Joubin 1888; Rauck 1976). The second parasite is located in the sensor channels of the fishes head, namely in the cavities of the frontal bones of fishes of the genus *Sebastes*. Here a hematoma is also formed around the parasite.

Parasitic copepods affect the internal organs of the hosts. Representatives of Lernaeoceridae often penetrate into the abdominal cavity where cysts form around them, which press on internal organs impairing their normal activity. The head of *Haemobaphes diceraus* reaches the aortic bulb or ventricle of the heart of Alaska pollack, *Theragra chalcogramma*, with the neck in the abdominal aorta or in one of the gill arteries and emerges in the gill cavity, forming an inflamed wound (Kazachenko 1969; Grabda 1975). Copepods, *Cardiodectes meduseus*, [can also] penetrate the heart cavity of the fish directly (Moser and Taylor 1978). The aortic bulb changes shape. Under the influence of the copepod *Lernaeocera branchialis*, the caliber of the bore is reduced and sometimes thrombosis of the blood vessels is observed (Grabda 1977).

Copepods affect the liver, kidney, spleen, intestines, hypophysis, and blood vessels, penetrating into these organs, reducing them, and causing hemorrhages (Bauer et al. 1977; Goreglyad 1955; Musselius 1973; Dzidziul 1973; Grabda 1975; Joubin 1888; Khalifa and Post 1976; Nataraian and Balakrishnan 1973).

Parasitic copepods are able to injure the skeletons of their hosts as well. Those which can do so are *Lernaeolophus sultanus* and *Vanbenedenia kroyeri*; but usually they are the representatives of the Philichthyidae family which can cause proliferation of the bony tissue and thrombosis of the sensory canals simultaneously (Grabda 1972; Kabata 1970; Quignard 1968).

Parasitic copepods alter the blood composition of fish (Denisov 1977; Pronin et al. 1975; Einszporn-Oreska 1973; Kabata 1970; Mann 1964; Nataraian and Balakrishnan 1977; Srinivasachar and Katre 1975). The data on this question, however, are contradictory and further investigations are needed.

Parasitic copepods do not always cause significant damage to their host, as is the case with *Pennella hawaiiensis* where the body condition of boarfish infected by this parasite did not decrease (Kazachenko and Kurochkin 1974). This phenomenon was observed repeatedly and fish infected by immature copepods had greater weight. When the copepods matured, the fish's weight decreased. A similar picture was observed in other features as well (percentage of total fat, percentage of fat in the kidney, and hemoglobin content) (Dzieuzeide and Roland 1956; Kabata 1958; Mann 1964; Nataraian and Balakrishnan 1977).

2) The role of parasitic copepods in ecosystems.

According to Bauer, the role of parasitic copepods in aquatic ecosystems is determined by 1) their role in elimination of hydrobionts; 2) their influence on the growth rate and conditions of hydrobionts; 3) their influence on the reproductive systems of hydrobionts; 4) their influence on the productivity of reservoirs; and 5) their role in the trophic chains of the ecosystem. However, in relation to parasitic copepods, not all the above-mentioned aspects of their roles in the ecosystem have been adequately studied. We have already discussed some of them.

The role of parasitic copepods in eliminating their hosts is most clearly revealed as a result of heavy infections of hosts (Khalifa and Post 1976). The majority of such cases are known from artificial fish rearing [aquacultural situations] (Slinn 1970; Urawa et al. 1979; Matumoto 1980). It is difficult to detect and record fish deaths caused by parasites in the seas and oceans, but some indirect data show this feature (Kabata 1970; Gjøsaeter 1971; Moser and Taylor 1978). For example, Kabata found that rockfishes of smaller sizes are more [heavily] infected by the endoparasitic copepod *Sarcotaces arcticus*. Therefore, he assumed that in [natural] fish populations a large percentage of fry die due to the pathogenic influence of parasites. Similar results were obtained in *Antimora rostrata* infected by *Sarcotaces komai* (Avdeev 1975) and in Alaska pollack infected by *Haemobaphes diceraus* (authors' data).

Fish mortality may increase during secondary infection when protozoa and fungi appear in wounds inflicted by copepods (Musselius 1973; Khalifa and Post 1976; Nigrelli and Firth 1939; Schaperclaus 1954).

Castration of hosts, decrease of the numbers of spawning fish, or retardation of spawning time are among the mechanisms by which parasitic copepods may influence the populations of their hosts (Giard 1888; Gjøsaeter 1971; Moser and Taylor 1978). The weight of gonads of infected fish is less than that of noninfected ones (Nataraian and Balakrishnan 1977; Kabata 1958).

Parasites may cause changes in fish behavior (Cheng 1973; Limbauch 1961;[5] Losey 1971). Very often infected fish prefer water with low oxygen content and choose places where there are many fish cleaners which collect parasites from infected fish. Infected fish display unnatural behavior, jumping out of water, etc. Sometimes fish of a species may clean parasitic crustacea from infected individuals of the same species (Hotta 1961; Kabata 1970; Kollatsch 1959).

In commenting on the role of parasitic copepods in ecosystems, one should not forget that they form a certain production, themselves, which contributes to the total production process [productivity] of the reservoir. Copepods produce a great number of eggs and free-living larvae. [Only] a small percentage of this biomass enters its host fishes, eventually supporting the continuation of the species. The remaining portion either enriches the reservoir by biogenes or is used as food by other hydrobionts. For example, parasitic copepods compose a constant part of the food of some fish, i.e., remoras (Cressay and Lachner 1970).

[5]Probably Conrad Limbaugh (1961) who wrote on "cleaners" during this period.

3) The significance of parasitic copepods for the fisheries.

This aspect is a constituent part of the questions discussed above. We have already cited examples of the negative influence of parasitic copepods on some organs and tissues, as well as on the entire fish organism and their populations. Ultimately all of this influences the fish productivity of reservoirs [all types of bodies of water]. Kabata (1955) provided the following figures: If every copepod causes a decrease in the weight of the whiting of 1 oz (28.3 g), the yield of the Scottish fishery would be reduced by 1,660 tons of fish. In the Hawaiian boarfish fishery, it was found that the muscles of a great number of fish contained large, dark, consolidated inclusions which were found to be the parasitic copepod *Pennella hawaiiensis*. In this connection the marketing of boarfish has been halted in order to clarify the etiology of infection. *Caligus macarovi*, parasitizing saury, is one of the economically important parasites. Saury products are sometimes rejected as defective because of the presence of this copepod.

We have already mentioned the role of parasitic copepods in artificial fish rearing. For example, such potentially dangerous copepods in the Pacific Ocean for salmons are *Lepeophtheirus salmonis* and species of the genus *Salmincola*; for flounders—*Acanthochondria cornuta*, *Lepeophtheirus hospitalis*, *L. parvicruris*, *Pseudolepeophtheirus longicauda*, *Nectobrachia indivisa*; and for the genus *Sebastes*—*Brachiella robusta*, *Chondracanthus pinguis*, *Clavella parva*, *Colobomatus kyphosus*, and *Naobranchia occidentalis*. *Caligus orientalis* may cause deaths of cultured fish as well.

4) Application of parasitic copepods to solving scientific practical problems.

In a sense we mean the use of parasitic copepods as biological tags. Local fish stocks have been investigated with the help of such biological tags (Dogiel 1962; Dogiel and Bykhovski 1939; Kovaliova 1965; Konovalov 1967, 1971; Kulachkova 1977; Mamaev et al. 1959; Nikolaeva 1963; Petrushevski 1940; Polianski 1958; Popov et al. 1980; Pronin 1965; Schulman 1963, 1968; Schulman et al. 1959; Gibson 1972; Kabata 1959, 1963; Mackenzie 1974; Margolis 1963; Sindermann 1957a, b, 1961; and others).

Parasitic copepods have been repeatedly used as biological tags both individually and together with other parasites. *Lernaeocera branchialis* was found to be an indicator of cod stocks. Fish are infected by this parasite mainly off the coasts [in coastal waters]. Fish inhabiting deep waters are either not infected or infected only weakly in comparison with coastal fish (Broek 1978, 1979; Sherman and Wise 1961; Sproston and Hartley 1941; Templeman and Fleming 1963; Templeman et al. 1976). Another species of parasitic copepod, *Phrixocephalus cincinnatus*, also provides the possibility of differentiating the stocks of halibut, *Atherestes stomias* (Kabata and Forrester 1974).

Also, differences in the rate of infection of fish enable us to assume that there are differences between hosts at the population level (Shotter 1971). Different saury stocks in the Pacific Ocean have different levels of infection of the same copepod species (Sokolovski 1969).

Specific Features of the Distribution of Marine Parasitic Isopod Crustaceans of the Family Cymothoidae (Isopoda, Flabellifera)

V. V. AVDEEV[1]

Nearly a century has passed since publication of the last of four monographs by Schioedte and Meinert (1884) concerning parasitic isopods of the suborder Flabellifera. In that summary work descriptions and redescriptions of 142 isopod species were presented along with data concerning the places of their discovery. During this century, a significant number of works on the fauna of the isopod groups of different areas of the World Ocean under consideration have been published, as were descriptions of more than 90 new species. However, until now there have been no works attempting to synthesize the data available about the places of discovery of parasitic isopods of the suborder Flabellifera in order to learn the rules of [rules governing] their geographical distribution.

Processing of the large amount of data on isopods available at my disposal (involving analysis of 55,917 specimens of more than 600 marine fish species collected during 85 cruises, as well as the analysis of data in the literature on this parasite group), allowed me to consider their distribution.

The objects of my investigations were isopods of the family Cymothoidae, which parasitize the gill-mouth cavity of fish or form zoocecidium [zooecidium or zooecidia] in the body wall of their hosts.

Examination of the geographical distribution of Cymothoidae in both meridianal [longitudinal] and latitudinal directions disclosed that the marine fauna of these isopods is subdivided into two ecological-geographical groupings, unequal in size. The first grouping, which includes a vast number of cymothoid species, is noteworthy for its distribution within the coastal zones of continents and insular archipelagos. The characteristic features of the second grouping (represented only by the genus *Glossobius*) is its distribution not only in the coastal zone but in the open sea as well.

The reason for such a division of marine Cymothoidae lies in the historically established [evolutionarily established] two trends of formation of the host circle [their circle of hosts]. As my investigations showed, the first (and main) trend is characterized by specialization of these isopods for parasitizing coastal fishes. The second trend is the result of the separation of another Cymothoidae group (small in number of species) from the main trend toward specialization for parasitizing coastal-oceanic and primarily, oceanic fishes. The reason for this phenomenon is the [relatively] recent transition of the ancestors of the flyingfishes (representatives of the genus *Glossobius*), which are the principal hosts, to residence in the epipelagic zone of the open ocean.

In most cases the association of Cymothoidae with tropical fishes turned out to be the factor determining the distribution of the predominant number (80%) of isopod species in the tropical region of the World Ocean. Some of these isopods, having certain eurythermal features and flexibility in selection of the hosts, penetrated into subtropical parts of the boreal and antiboreal regions.

Such penetration became possible as a result of the inclusion of subtropical and moderate-warmwater fish species within the circle of hosts. Further penetration of isopods into boreal (7 species) and anti-boreal (4 species) regions may be explained, on one hand, by the inclusion of fish residing in moderate and moderate-cold waters among their number of hosts; and on the other hand, by the availability of regularly occurring translocation of warm waters (currents) in the meridianal [or longitudinal] direction.

The examples are: 1) Penetration of the Cymothoidae, *Lironeca vulgaris*, into the boreal region where it began parasitizing fish of the families Merlucciidae and Hexagrammidae, and 2) penetration of the isopod *L. raynaudii*, which employs representatives of the family Nototheniidae, common in Antarctic and sub-Antarctic waters as hosts, into anti-boreal regions.

For example, I may note that in the boreal region of the western Atlantic, the distribution of Cymothoidae coincides with the zone of the warm current—the Gulf Stream, which is a component of the northern subtropical anticyclonic circulation. Originating in the tropical region, this current flows along the coast of North America up to about Cape Cod. This favors the northward penetration of the tropical hosts of both ecological and geographical groupings of Cymothoidae. Further, when the current turns eastward into the open ocean, only one of the two representatives of the second ecological and geographical grouping, *Glossobius impressus*, penetrates there.

Cymothoidae are totally absent from the Arctic and Antarctic regions.

The reasons for the latitudinal distribution [extent] of the area in which isopods of the family Cymothoidae occur in the following four coastal areas (where a high level of endemism or isolation is observed) are: 1) The coastal character of the distribution of the main number of marine Cymothoidae species; 2) existence of the overwhelming number of their hosts in warm waters (or in moderate-warm waters); as well as 3) the meridianal [or longitudinal] orientation of continents (as the limiting factor), (see Fig. 1).

I. The area [the Indo-West Pacific] from the Cape of Good Hope, including the Indian Ocean coasts of Africa and Asia, the Pacific Ocean coasts of southern and western Asia (up to Ayan in the Sea of Okhotsk), the Indo-Malayan Archipelago, the islands of Hawaii and Samoa, and the coasts of Australia and New Zealand.

II. The area of the Mediterranean Sea and the Atlantic Ocean coasts of Europe and Africa, approximately from lat. 48°N southward to Angola.

III. The area of the Atlantic Ocean coasts of North and South America from Cape Cod southward to Rio de Janeiro.

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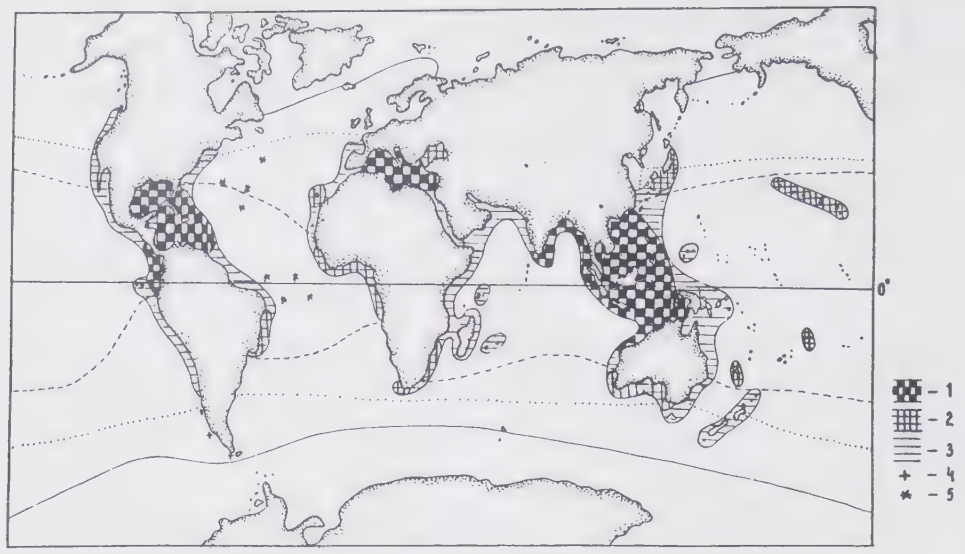

Figure 1.—The present distribution of marine isopods of the family Cymothoidae. 1 = places of the most abundant distribution of endemic species and genera; 2 = places of individual distribution of endemic species and genera; 3 = distribution of widely observed endemic species; 4 = places of observation of endemic *Lironeca raynaudii* in sub-Arctic waters; and 5 = distribution of the genus *Glossobius* in epipelagic zones of the open ocean.

IV. The area of the Pacific Ocean coasts of North and South America from lat. 48°N southward to Valparaiso (Chile).

As I noted earlier (Avdeev 1979), these special features of the geographical distribution of isopods of the family Cymothoidae in the latitudinal direction [i.e., north-south] developed as a result of the fact that the natural barrier to the hosts' penetration (along with the orientation of the coasts of the continents meridianally) was water temperature. The depths also interrupted the distribution latitudinally even where favorable temperature conditions exist.

Comparison of the Cymothoidae distribution list disclosed a very weak community [commonality] of Cymothoidae fauna at the species level between the above-mentioned areas. Thus, in the first area, 71 of 75 species are endemic; in the second, 13 of 15; in the third and fourth, 11 of 14 and 7 of 9, respectively. Five Cymothoidae species were recorded as occurring simultaneously in two areas. Two of them belong to the genus *Glossobius* (the parasites of flyingfishes, which accomplish large migrations). There was no species common to all four areas!

Existence of a great number of endemic species of isopods in the distributional areas indicated for the Cymothoidae (i.e., the areas with essentially isolated faunas) and of endemic genera in two of them demonstrates the existence of the four independent centers of the formation of species of parasitic isopods. In actually fixing the location of these centers, the nature of the distribution of the endemic species and genera was taken into account in order to discover the places of their greatest concentration.

Of the 71 known endemic species of the first area (i.e., the entire Indo-West Pacific), 37 are distributed in the Indo-Malayan Archipelago while 18 species reside in the Red Sea, South and southeastern Africa, southern and southwestern Australia, Japan, the area of Ayan in the Okhotsk Sea, Hawaii, New Caledonia, and Samoa, places distant from the location of the main Cymothoidae concentration. The other species endemic for this area are widely distributed throughout the area. The distribution of the endemic genera shows (as in the case with the endemic species) that the Indo-Malayan Archipelago is the place of their highest concentration. Eleven of 12 Cymothoidae genera are registered [recorded] from this region.

The place of residence of the largest number recorded in the second area (i.e., the Mediterranean Sea and the Atlantic coast of Europe and Africa, including the area from the English Channel southward to Angola) is the Mediterranean Sea, where 13 of 15 species are registered.

The third area, encompassing the Atlantic coast of America from Cape Cod down to Rio de Janeiro, has the Caribbean Sea as the place [center] of distribution of 8 of the 11 endemic species. The other species are recorded from the coast of Brazil.

Five of seven endemic Cymothoidae species of the fourth area, encompassing the Pacific coasts of North and South America from lat. 48°N to Valparaiso, are distributed from the boundary between Ecuador-Peru northward to about Los Angeles. The distribution of the other two species endemic to this area along the coasts of Panama and Ecuador allows me to consider the tropical coasts of Central and South America as the place of the greatest concentration of endemic Cymothoidae fauna.

Thus, the following centers of Cymothoidae species formation are revealed: Indo-Malayan, Mediterranean, Caribbean, and tropical eastern Pacific (Fig. 2).

Speaking about the pathways of Cymothoidae distribution in the World Ocean, it is necessary to point out that the Indo-Malayan center has historically established conditions differing from those in other areas. Cymothoidae in the other areas were able to expand in a meridianal [longitudinal] direction from their centers of formation only along the coasts of Africa, Europe, and North and South America (because of the depth barrier). In the Indo-West Pacific the coastal hosts penetrate significant regions in both meridianal and latitudinal directions. This occurs because of the location [and orientation] of the Indo-Malayan Archipelago at the boundary between the Pacific and Indian Oceans and the formation by the continents and insular archipelagos of a continuous zone of coastal shoals in all four directions, together with

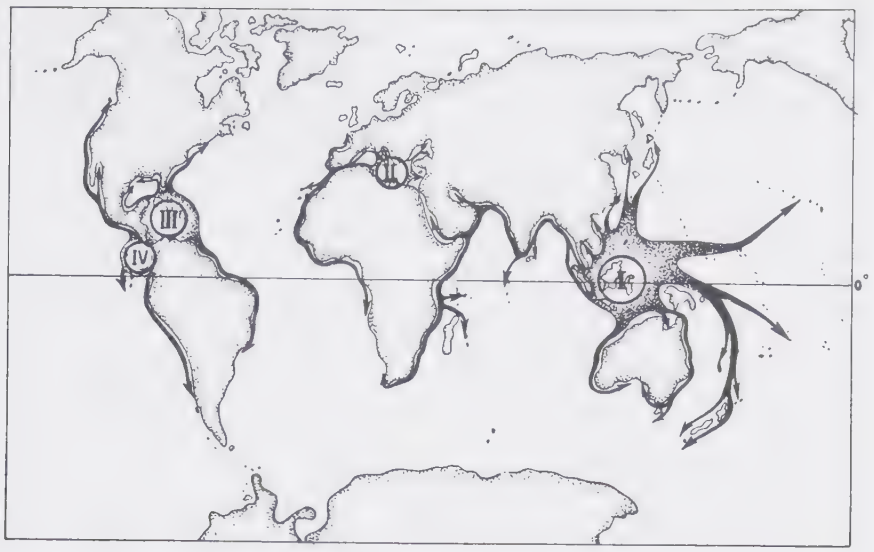

Figure 2.—The present centers and pathways of distribution of isopods of the family Cymothoidae in the World Ocean. I = Indo-Malayan; II = the Mediterranean; III = the Caribbean; and IV = tropical eastern Pacific.

the shoals being separated from each other only by relatively short distances. As a result of this, the Cymothoidae recorded from the Indo-Malayan Archipelago are also distributed off the eastern coast of Africa, Japan, Hawaii, New Zealand, etc.

The distribution of the cymothoid *Ceratothoa oxyrrhynchaena* off the coast of southeastern Africa, in the Red Sea, and in the Mediterranean Sea demonstrates the increase in the geographical range of distribution of Cymothoidae (to the area of the southern coast of Africa) which became possible due to human economic activity—the building of the Suez Canal.

The present distribution of the main group of Cymothoidae species in the tropical region of the World Ocean provides the basis for connecting the origin of these isopods with the existence of the former Tethys Sea, which had its maximal dimensions during the entire Mesozoic era and the early tertial [Tertiary] period (being the warm one) (Ekman 1953). The four centers of residence of the present day Cymothoidae, which I have managed to discover, coincide perfectly with their dislocation. This is, in its turn, in full conformity with the conclusion by Kusakin (1979) that the tropical shelf is the most ancient place of the species rests [is based] upon the most primitive suborder, Flabellifera.

Due to the pelagic life history of the ancestral hosts, the ancestral Cymothoidae had a wide distribution in the Tethys Sea during the Cretaceous period. During that period some portion of Cymothoidae ancestors penetrated the fresh waters and, thus, gave birth to the formation of the freshwater fauna of the family Cymothoidae.

The important basis for realization of the picture of the origin of the marine fauna of Cymothoidae is the establishment of the historical perspective of their specific formation and the pathways of their distribution. In order to settle this question it is necessary to refer to the principal peculiarity of the distribution of present day isopods—the existence of the four essentially isolated (at the specific level) regional and endemic faunas of these parasites, each of which has its own center of distribution. Undoubtedly, one of them should have been [or was] the place of formation of the Cymothoidae fauna.

I may judge the relative antiquity of the present centers of Cymothoidae distribution from an analysis of the faunas based on the rank and level [degree] of endemism revealed. The results showed that the Indo-Malayan center has the most endemic species (37) and the overwhelming number of endemic genera (11) of Cymothoidae. The prolonged process of species formation which resulted in the establishment of an unusually high level of endemism of isopods at the species and genus levels undoubtedly indicates that I deal with the most ancient area of the distribution of these isopods.

The lower number of endemic species (13) and genera (2) in the Mediterranean Sea indicates that this center of Cymothoidae distribution is younger [than the Indo-Malayan]. The absence of endemic genera testifies that the reservoir of the Caribbean Sea is younger still. In the tropic and East Pacific center I obviously deal with the youngest Cymothoidae fauna, which was formed during the end of the Pleiocene when the development of the Isthmus of Panama (Ekman 1953) separated a part of the tropical Central American fauna.

My conclusion that the Indo-Malayan area is the historical center of formation of the Cymothoidae fauna may be objected to on the basis that domination of endemic species and genera of isopods in that area could be a result of the stable climate persisting there throughout the Tertiary and Quaternary periods. This was favorable not only for continuance of the tropical fauna of the Cretaceous period, but also for its prosperity nowadays (Ekman 1953). On the other hand, the very rich tropical fauna of the Mediterranean Sea, which developed during Pleiocene and Pleistocene periods, was ruined because of the Ice Age. That is why it is quite possible that this very area was the ancient center of formation of the Cymothoidae fauna. However, if this point of view is possible when considering other groups of animals (e.g., the existence of relicts nowadays in the Mediterranean Sea, Ekman 1953) it will not suffice in relation to isopods of the Cymothoidae genera.

Of the eight Cymothoidae genera occurring in the Mediterranean Sea, six are recorded also in the other three areas. Further-

more, their composition includes the three most abundant and ancient specific genera—*Lironeca*, *Cymothoa*, and *Ceratothoa*. The representatives of two other monotypical genera, *Mothocia* and *Emetha*, are morphologically close to isopods of the genera *Lironeca* and *Ceratothoa*, respectively.

Thus, specific features of the geographical distribution of Cymothoidae argue in favor of the Indo-Malayan Archipelago as the center of faunal formation of this group of parasitic isopods.

The area is possibly [probably] the historical place of formation of the entire fauna of all the isopod species. I may conclude this on the basis of the features of the present distribution of the representatives of the primitive families, Cirolanidae and Sphaeromatidae. As Kusakin (1979) pointed out, these isopods are totally absent in the Arctic and their level of penetration into boreal waters is very low. Even so, in the Southern Hemisphere they are represented in great numbers not only in boreal but also in antarctic waters.

Such an asymmetric pattern of distribution of primitive isopods would have been formed only under similar earlier conditions. To my mind one of them should have been the location of the most ancient center of formation of fauna of isopods in the tropics directly close to the Southern Hemisphere. Of the four existing centers of Cymothoidae distribution, only the Indo-Malayan meets these requirements. Moreover, if I retain the scheme by Levites (1961) concerning the distribution of the four continents in the Carboniferous (the time of the most ancient finds of fossil isopods), then the above-mentioned center of the distribution of parasitic isopods lay in the area adjacent to the eastern part of Gondwana. All the conditions for free penetration of ancestral isopods in the southern direction existed there, while the opportunity for their distribution from other centers was provided later, after the disintegration of the megacontinent—Gondwana—and formation of the Indian and Atlantic Oceans.

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Pigmented Macrophage Accumulations (MMC; PMB): Possible Monitors of Fish Health[1]

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ABSTRACT

Anthropogenic pollution of the World Ocean is a growing problem. Areas most heavily contaminated are often sites where many important fishes grow and reproduce. It is not easy to relate levels of pollution to diseases and fish mortalities in nature and, though it has been done in but few cases, circumstantial evidence in many others is very strong.

Environmental pollution has direct (acute) and indirect (chronic) effects, i.e., causing deaths quickly as well as increasing diseases, causing other debilities, and reducing reproduction, but evaluation of these effects is difficult. Histopathological examination of representatives of stressed populations, the most useful technique for establishing or monitoring the disease-related effects of pollution, is difficult, costly, and time consuming. More efficient health-monitoring systems or indicators are needed.

The characteristics and capabilities of a suitable system are discussed. After examination of the reticuloendothelial system of higher fishes, the visceral macrophage response systems (i.e., the melanin-macrophage centers—MMC, and the pigmented mictic bodies—PMB) of these fishes appear to have those qualities needed for a relatively efficient health monitoring system. Investigations into applicability of these systems as indicators of fish health are in order since it appears that such an approach would be more productive than classical blood chemistry determinations.

INTRODUCTION

Anthropogenic pollution of the World Ocean is a growing problem. It is attributable to increasing industrialization but is related as well to the outdated concept that the oceans have an unending ability to accept waste. The effects of this pollution are manifold, but certainly nowhere more apparent than on the productivity of animal life. It is ironical that the points of heaviest pollution should also be sites for reproduction and growth of many of the most important commercial fishes. Pollution, however, is not confined to such "nurseries" of fin and shellfish. Deep ocean dumping of wastes also raises the levels of various pollutants to which finfish are exposed.

Toxicity of most pollutants, which include such substances as petroleum-derived hydrocarbons, heavy metals, insecticides, herbicides, and sewage, have been examined in the laboratory and their LC50 and/or chronic effects for fish and shellfish determined (National Science Foundation 1974; Environmental Protection Agency 1979). Correlation of these data with decreasing populations of fish on a worldwide scale is much more difficult. Some mass mortalities and individual decreases in numbers of fish have been observed and documented, but determining the general health of fish over broad geographic areas is not easily achieved and not well documented (Brown et al. 1970; van Loon and Beamish 1977; McFarlane and Franzin 1978; Gray 1979).

A healthy organism is an organism in physiological balance with its environment. Disease, on the other hand, is an ongoing process which results in upsets to the physiological balance, upsets in homeostasis, and upsets in the relationship of the organism and its environment. Initially these imbalances are at the biochemical level, eventually they become functional and morphological. It is this whole concept of pathogenesis and its resulting chemical and anatomical changes that are of interest to the pathologist.

The disease process brought about by the toxicant may manifest itself on any of the aforementioned levels, or, in fact, it may be related with a natural disease which masks the effects of the toxicant per se. At best, the toxicant results in pathognomonic lesions and the condition is easily identified as to cause and readily classified as an "environmental" disease (Wolke et al. 1975, Sindermann 1979). Unfortunately it appears that diseases of this sort are relatively few and that toxicant lesions are often quite nonspecific. Coupled with this nonspecificity is the fact that the levels of the toxicant to which the fish is exposed in the marine environment are far less than those studied in the laboratory. There is mounting evidence, however, that these chronic subclinical levels, while not readily lending themselves to detection in terms of host response, increase disease susceptibility resulting in increased prevalence of disease processes and parasite burdens in exposed populations (Ziskowski and Murchelano 1975; Mearns and Sherwood 1977; Overstreet and Howse 1977; Welling et al. 1977). This introduces the concept of an "environmentally associated" disease in which the noxious agent has an indirect rather than a direct effect—a more realistic concept [than others] which is based upon the multitude of information from necropsy examinations which have been conducted on marine fish from "polluted" and "nonpolluted" sites.

Evaluation of these subtle effects on the health of fish, considering in turn their genetic variability and the variability of their environment, appears difficult. Classical methods used to determine the health of higher vertebrates, such as blood chemistry

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determinations, might be of assistance if sufficient base data could be collected. Unfortunately, tests of this nature have shown tremendous variability among individuals of the same species, requiring large numbers of determinations to achieve statistical significance. When this observation is coupled with the variability among families and geographical locations, the approach seems impractical. Given time, much base data could be collected, but a problem of such international concern does not allow the luxury of time.

Histopathological examination of group representative individuals is more informative as a monitor of health, but is logistically impractical and may not reveal even those nonspecific lesions of toxicants previously discussed. Histopathology as a technique, however, may be of value, especially if it is used to examine a specific system sensitive to a wide range of insults.

Availability of a more effecient system to monitor the health of fishes in relation to the environment is important. Such a health monitoring system must have certain qualities. First, it must be a system which is common to all fishes, regardless of their source. Second, it must be basic, and by basic is not meant unsophisticated but rather a system which is first in the chain of events following an insult. In this sense then, the system should be rapidly responsive in reflecting upsets in homeostasis and the presence of foreign antigens. Also, the proposed system should reflect or presage early tissue damage. The third quality is accessability. This is the ease with which the system is examined by the investigator and the speed with which data can be generated.

The purpose of this paper is to suggest a system which might be used for the monitoring of fish health. While studies have shown the proposed system to have the necessary qualities it has not yet been used as a monitor, thus the feasibility of the hypothesis proposed here remains to be tested.

RETICULO-ENDOTHELIAL SYSTEM

The reticulo-endothelial system (RES) of the fish is sophisticated and highly functional (Ellis 1974). It is similar, but not identical, to Aschoff's RES in homeotherms (Aschoff 1924). The systems differ in that the fish has phagocytically active cells lining the atrial endocardium and serving as a supportive endothelium (pillar cells) in the gill (Ferguson 1975; Chilmonczyk and Monge 1980). In addition, accumulations of pigmented macrophages are randomly distributed in the hepatic, renal, and splenic parenchyma. Kupffer cells are absent or, if present, are only weakly functional.

The relationship of the fish RES to the homeotherm Mononuclear Phagocyte System (MPS) of van Furth is uncertain at present (van Furth et al. 1972). The MPS does not include facultatively phagocytic cells, i.e., reticular cells, fibroblasts, and, most importantly, endothelial cells. Light microscopic examination of fish atrial endocardium reveals cells morphologically identical to classical endothelial cells. These cells have the capacity to hypertrophy, acquire a rounded profile, and phagocytize blood-borne particulate matter. This phenomenon may be elicited by simply inoculating carbon particles intraperitoneally in higher teleosts. The mechanisms by which these cells are excited and their facultative nature are unknown. Further, there are other criteria used to classify phagocytic cells for inclusion in the MPS. Such cells must contain receptor sites for immunoglobulins and complement on their cell surfaces. A small percentage of macrophages in plaice spleen and kidney have surface immunoglobulin (Ellis 1974). The presence of these receptors on other fish phagocytes needs to be determined.

PIGMENTED MACROPHAGE ACCUMULATIONS

Groups of pigmented macrophages, present primarily in the liver, spleen, and kidney, are an important component of the fishes' RES. These structures were probably first described by Jolly in 1923 and were later considered by Roberts (1975) who coined the term melanin-macrophage centers (MMC). Still later, Agius (1979b, 1980) carefully described morphological species differences and pigment content of the accumulations. Other workers who have described these structures, which occur in amphibians and reptiles as well, include Yoffey (1929), Mackmull and Michels (1932), Ellis et al. (1976), and Ferguson (1976).

In the higher Teleostei the accumulations vary from a few to a large number of cells forming rounded islands 40 to 1,000 μm in diameter. The edges of the islands are usually regular and in some instances the accumulation may have a degree of encapsulation. These fibers have been described as argyophilic (Roberts 1975). A thin rim of lymphocytes may be found surrounding the accumulations (Fig. 1).

Cells within the aggregates are primarily macrophages with irregular, poorly defined outlines and vesicular nuclei. Their cytoplasm contains black to yellowish pigmented material and/or phagocytized organisms. The cells vary in size from 10 to 30 μm. There are also present a few true melanogenic cells (melanocytes). These are smaller (7 to 15 μm) and their cytoplasm is heavily laden with brown to black granules.

Ultrastructurally the macrophages are not morphologically unique. The nucleus is often kidney shaped or indented and chromatin frequently lies just inside the nuclear membrane. The usual complement of organelles lie close to and surround the nucleus. Golgi complexes are common. Much of the cytoplasm is occupied by vacuoles and lysosomes. Pigment, when present, is found within membrane-bound vacuoles (melanosomes, ceroid).

The general color of the accumulations in higher fish tends to be yellow brown. Their distribution is random (perhaps with some tendency to accumulate nearer blood vessels) in the parenchyma of liver, spleen, and kidney (anterior and posterior). However, in certain pathological processes their distribution is far more wide-

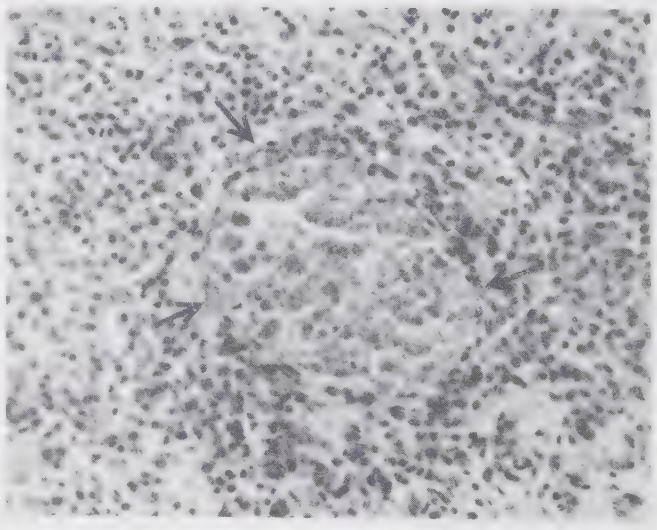

Figure 1.—Macrophage accumulation (MMC; PMB) in spleen of a higher teleost (*Lepomis macrochirus*). Note round shape, slight fibrous encapsulation, and thin rim of lymphocytes. Hemotoxylin & eosin × 121.

spread, including the gastrointestinal tract, peritoneum, and connective tissue.

The general microscopic appearance of macrophage accumulations may differ in certain fish and early investigations seem to indicate a relationship to evolutionary development (Agius 1980). In the salmonids the accumulations are smaller, more irregular in outline, and much darker (Fig. 2). As in higher fishes both macrophages and melanocytes are present, however the latter comprise a far larger proportion of the cells than in the centers of higher fishes.

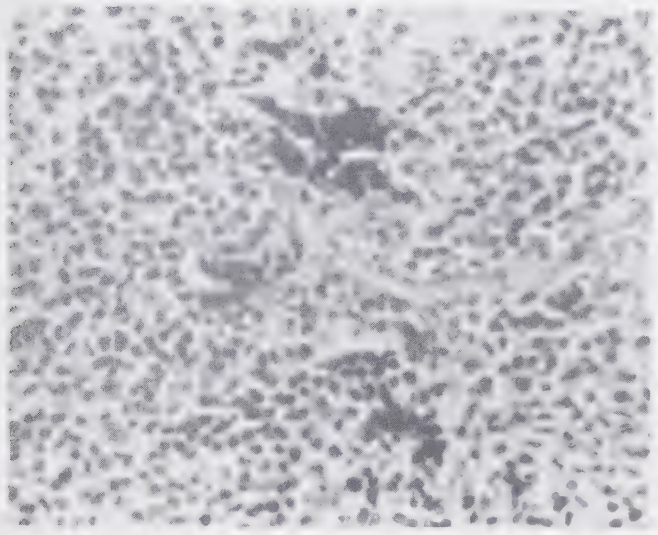

Figure 2.—Macrophage accumulations (MMC; PMB) in the spleen of a salmonid (*Salmo gairdneri*). Note irregular shape and dense melanization. Hemotoxylin & eosin × 308.

PIGMENTS

The pigments contained in the macrophage component are identifiable by means of light microscope histochemistry and electron microscopy. The pigments can be identified as hemosiderin, melanin, and ceroid.

Hemosiderin

Hemosiderin is an endogenous hemoglobin-derived storage form of iron. It is, therefore, a normal and important constituent of the body and of hemoglobin metabolism. When red blood cells are destroyed, hemoglobin is degraded to iron, biliverdin, and globin. The iron, as ferritin or bound to transferrin within the macrophage, is stored in the spleen or moved to sites of red blood cell formation. It is known as hemosiderin and is seen as brown to black intracytoplasmic granules. Its presence in the spleen is normal, both in fish and homeotherms. Special staining techniques may be used to identify and better outline the deposits. The Prussian blue method (potassium ferrocyganide) stains the granules a bright blue (Thompson 1966).

Excessive accumulations of the pigment or accumulations in other organs is known as hemosiderosis and reflects a pathological process. The condition may be metabolic in origin, but in the vast majority of the cases it is due to a sudden breakdown in hemoglobin secondary to a hemolytic anemia.

Melanin

Melanin is a complex polymer of uncertain structure which may be formed from the amino acid tyrosine or the catecholamine epinephrine. It is a common pigment in the integument of most animals and results in a brown to black coloration (Riley 1980). Cells which contain melanin in the fish include the melanocyte, melanophore, and macrophage. It is not certain whether all three cells are melanogenic, the concensus being that the first two are, while the macrophage acquires melanosomes via an, at present, unknown transfer mechanism. This probably occurs when macrophages come in contact with dendritic melanophores and phagocytize portions of the cell or their extruded melanosomes.

It is interesting to note that relative amounts of melanin appear greater in the centers of cold-water fish or in fish kept at colder temperatures. This observation may relate to the suggested functions of the pigment melanin. The pigment appears to have two primary functions. First, protective and second, destructive. In the protective sense it is similar to alpha-tocopherol, an electron donor. This relates to its resonation with its semiquinone free radical precursor (Riley 1980). It can absorb free radicals or inhibit the propagation of the free radical chain reaction and will protect the cell from the reactive substances produced during lipid oxidation (Edelstein 1971). Its presence in a cell responsible for collecting effete lipids is self-evident.

Its second function, that of destruction, comes about by its ability to oxidize nicotinamide-adenine dinucleotide (NADH) and produce hydrogen peroxide, which, in conjunction with peroxidase and iodide, can be bacteriocidal, perhaps via halogenation of the bacterial cell wall. It can therefore function in destruction of invading microorganisms which have been ingested by the macrophage in a manner essentially similar to the generation of hydrogen peroxide by the probable NADH oxidase and halogenation in homeotherms. However, there is also the possibility that quinone precursors of melanin may serve a bacteriocidal function as well since quinones are strong oxidizing agents in their own right. Because the mechanisms by which melanin functions are nonenzymatic it is interesting to speculate that melanin plays an important role in the defense mechanisms of poikilotherms where enzymatic activity is so temperature dependent.

Ceroid/Lipofuscin

The third pigment commonly associated with visceral macrophage accumulations is ceroid or lipofuscin. This is a yellowish-green, autofluorescent age pigment. It is a breakdown product of lipid peroxidation and tissue destruction. Massive increases in this pigment are seen in vitamin E deficiency and/or rancid fat problems of fish (Poston et al. 1976; Watanabe and Takashima 1977; Roald et al. 1981).

FUNCTION

Information on the function of piscine visceral macrophage accumulations may be collected from studies of the fate of injected particulate matter and the types and functions of pigment present in the centers. Roberts in 1975 alluded to such a functional systhesis and recent investigations have added credence to this synthesis.

When particulate matter (carbon, latex beads) is inoculated interperitoneally or intervascularly the material is rapidly ingested by the various phagocytic cells of the RES (Mackmull and Michels 1932; Ferguson 1976; Ellis et al. 1976; Chilmonczyk and

Monge 1980). After ingestion, the laden macrophages migrate to visceral accumulations or begin new accumulations in the parenchyma of spleen, liver, and kidney. The speed with which this is accomplished appears related to the route of injection and to temperature. When the stimulated macrophages reach the centers they are not simply added to the surface of the accumulation but are found to mix with the other cells so that one can appreciate the accumulations as a dynamic moving body. This has led George and Agius to suggest that these accumulations be referred to as "pigmented mictic (Gr = mixing) bodies" or PMB.

This movement of macrophages to a point of accumulation suggests that their function is to centralize foreign material for a number of purposes. First, to present such antigens to cells capable of producing humoral antibody, second, to remove toxic substances and to centralize their detoxification, and third, to store reuseable substances.

Further evidence for this hypothesis is found in the pigments present and their previously discussed significance. Ceroid and lipofuscins are peroxidation products, potentially capable of producing free radicals as well as reflecting tissue breakdown (Hartroft and Porta 1965). Ceroid is commonly stored in PMB. Melanin is capable of accepting dangerous free radicals and in destroying microorganisms. Melanin is found in macrophage lysosomes in relation to bacteria and ceroid. Finally, hemosiderin reflects red blood cell destruction, storage of reuseable iron, and, in hemosiderosis, hemolytic processes. Anemia is a common sign of disease in fish and often reflects the activity of endotoxins as well as some water-borne toxins.

METHODS

The visceral macrophage accumulations (MMC; PMB) of higher fish appear to have those qualities needed for a health monitoring system. They are common to all fishes and they are basic in that their macrophage component is first to come in contact with foreign antigens or remove endogenous and exogenous toxic substances to a centralized area. They collect pigments which reflect pathological processes and tissue destruction. Finally, they are easily accessible, requiring only routine histopathological methods for examination.

The literature is replete with studies that indicate increases in numbers of PMB in relation to age, starvation, disease, and dietary imbalances. There is a body of evidence that these structures reflect upsets in homeostasis and early disease processes (Roberts 1975; Agius 1979a; Agius and Roberts 1981).

It is suggested therefore that some effort be placed on investigating the use of these structures as indicators of fish health. It appears that such an approach would be more productive than classical blood chemistry determinations.

These structures will certainly lend themselves to mass determinations either by the point-counting planimetric method of Hennig (1958) following the reasoning of Chalkey (1943) or by means of colorometric assessment of the fluorescing ceroid within the centers. The latter method, however, essentially equates ceroid with mass and may prove to be specious.

Subjective evaluation of hemosiderin and melanin content may also be made, especially with reference to the organ in which the hemosiderin is found. It is suggested that all sections be routinely stained using the Prussian Blue reaction (Perls method for iron) and counter-stained with nuclear fast reds. The macrophages are apparent as pale yellow accumulations, melanin is black to brown, and hemosiderin bright blue. All three pigments are therefore rapidly and easily visualized. Objective evaluation of these pigments in individual centers may also lend themselves to colorometric determinations.

The authors recognize that measurement of the suggested system, because of obvious variables, may in fact be difficult. Investigators should recognize that the mass of PMB will vary as to age so that base data must, as in other systems, be collected. These data can be taken from only one species at a time and from a species inhabiting an environment as pristine as possible. Statistical questions must be answered regarding numbers of sections, numbers of organs, and surface area to be examined. These do not seem, however, to be insurmountable problems and it is felt that investigation of the use of PMB as monitors would be worthwhile.

If figures could be generated indicating mass and pigment content/age class/species these data could then be compared with data taken from smaller numbers of the same species in other geographical areas. The hypothesis could be tested by examining populations from known polluted sites. If statistically significant differences were present then relatively rapid surveys of important geographic areas could be conducted to determine if heretofore unsuspected stresses were being applied to indigenous populations.

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Infectious Diseases of Fish Involved in Marine Aquaculture in the Soviet Far East

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Intensive development of aquaculture in the Soviet Far East results from the complex of factors favorable for the progress of this prospective branch of the national economy. The culture of salmon, mollusks, algae, etc., is not only possible but highly profitable.

Among the problems of the development of intensive aquaculture, that involving the protection of cultured fish from infectious diseases which can cause great losses, is of major importance.

Prophylactic treatment of fish against infectious diseases in aquaculture is one of the important conditions for successful economic management and its profitability. Rich aquaculture experience accumulated in the Pacific basin countries (Canada, U.S.A., Japan and others) clearly demonstrates the necessity of studying the infectious diseases of maricultural organisms and of developing methods for diagnosis and preventive treatment of disease.

In this connection the Laboratory of the Infectious Diseases of Mariculture Objects (TINRO) began to investigate infectious diseases of salmons and bivalves, as the most important organisms of the Soviet Far East. Preliminary data acquired while examining healthy and infected fish and mollusks are presented in this paper.

During April and May of 1980 an epizootic disease of the fry of cultured coho salmon, *Oncorhynchus kisutch*, was observed at the TINRO geothermal station. Daily mortality during a single month was 1 to 2%, with increases in some days. Infected and dead fish had pale, swollen gills covered with mucus. Spots of yellow or yellow-orange color were easily seen in the mucus. Visible changes in the internal organs were not seen during autopsy. Using phase-contrast microscopy of unstained slides of the gills, a great number of motile bacteria, as well as the destruction of gill filaments, were discovered.

Cultures of the motile, gram-negative bacteria, which developed successfully on cytophaga-agar, forming yellow pigment, were found on the gills and in the kidneys of dead and infected fish. The type of growth of the colonies is prostrate. The cultures grew well at a temperature of +5°C. The bacteria were gram-negative, motile, oxidase-positive bacilli able to grow without air. A typical feature of these cultures was bacterial mobility on the surface of the agar at the margin of the colony.

An epizootic disease with similar clinical and bacteriological features was also recorded among chum salmon fry cultured at the experimental TINRO station.

On the basis of these disease study data, we can conclude that in both cases it was the cold-water salmon disease, caused by flexibacteria.

Along with these investigations, the microflorae of scallops (*Patinopecten yess*) and oysters (*Crassostrea gigas*) were also studied. Upon studying the microflora of the scallop it was found that the infection level of its internal organs is heterogenous: Minimum microflora was on the muscle while the mantle and liver were more heavily infected. Qualitative variety of the microflora was most evident in summer, i.e., at high seawater temperatures. When water temperature decreased, the gram-negative microflora was displaced by a gram-positive one. A relationship between the environmental microflora and the microflora of the scallop organism was observed.

In August of 1980, oyster beds were investigated in Posyet Bay (South Primorye), where a considerable oyster mortality was observed. A great number of dead and injured oysters had also been discovered there on the collectors. Spots of black or brown-black color were seen on the internal surfaces of the shells, mostly in the zone of adductor muscle junction. No significant muscle changes were discovered. Bacteria of the genus *Vibrio* were mainly found in mantle, muscle, and liver. Some of them were luminescent. Other microflora was rather poor. Probably, the oyster mortality was caused by an intensive infection of the oysters with *Vibrio* spp., due to the over-density of mollusks on the collectors and high seawater temperatures.

The facts mentioned above suggest the necessity of further, more intensive studies of diseases of aquaculture organisms in the Soviet Far East.

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Recent Studies in the United States on Parasites and Pathogens of Marine Mollusks With Emphasis on Diseases of the American Oyster, *Crassostrea virginica* Gmelin[1]

WILLIAM J. HARGIS, Jr.[2]

ABSTRACT

Morphological, systematic, faunal, and life cycle studies predominated research on marine parasites and pathogens in the United States before World War II. Much was primarily basic or academic in nature. Since then it has grown and diversified under pressure of efforts to: 1) Increase yields of invertebrate-based fisheries, in nature and under controlled conditions; and 2) understand, protect, and improve the resources, estuarine and marine environments, and human health and welfare. Over the last 30 yr pathobiological investigations of economically and ecologically important marine invertebrates have broadened into submicroscopical anatomy (TEM and SEM techniques), physiology, immunology, genetics, host-parasite ecology, interactions between environmental pollution and disease, and prophylaxis and treatment of their diseases.

Importation of foreign oysters (and other shellfish species) and their transfer and transplantation between the coastal regions, provinces, and states of North America have resulted in growing disease problems and a corresponding interest in the parasitology and pathology of the mollusks involved. It has also spawned efforts to control introductions and transfers.

Two major diseases have been found to interfere with production of native Atlantic oysters along the Gulf and/or Atlantic coasts of the United States. These are the "Dermo" or "fungus" disease, caused by the apicomplexan protistan *Perkinsus marinus* (both coasts) and "MSX" or Delaware Bay disease, caused by the sporozoan *Haplosporidium nelsoni* (the Atlantic coast—principally in Chesapeake and Delaware Bays). Knowledge of these important epizootic-producing diseases is reviewed and discussed, along with that of other parasites and pathogens of molluskan shellfish in North America, and an extensive References section of the results of recent research on molluskan parasites and diseases is presented.

INTRODUCTION

Most of the research on parasites and pathogens of marine invertebrates has taken place in this century. Faunal, morphological, systematic, and life cycle studies predominated the literature before World War II. Much early work on parasites of invertebrates was primarily basic or academic in nature or on animals used in experimentation, but even then the necessity to explain unusual or catastrophic events, such as fish kills, major declines in fishery catches, impacts of plankton blooms (such as red tides and mahogany waters), the impacts of pollution on fishery populations, and other practical questions predominated.

Since World War II, research has increased markedly. More scientists and institutions are involved in pathobiology of marine vertebrates and invertebrates than ever before. Academic interest continues to be a force but the need to produce more shellfish (Mollusca and Crustacea) on a sustained basis from coastal and ocean waters and to protect the environment and human health have been primary factors prompting government support for these studies. The growth of commercial display aquaria and of laboratory experimentation with marine fishes and invertebrates has also encouraged interest in parasites and diseases.

New knowledge, techniques, and equipment have enabled pathobiological investigations to broaden into submicroscopic anatomy (i.e., studies of ultrastructure using scanning and transmission electron microscopes), immunobiology, immunochemistry, genetics, host-parasite ecology, microecology, physiological ecology, and research on techniques for prophylaxis and treatment of disease.

The development of marine aquaculture has increased the need to understand the impacts of parasites and pathogens on the marine invertebrates being used. Mollusks, being among the easiest of marine invertebrates to "farm" or bring under culture are of special interest. Most research activity on parasites and pathogens of this group centers upon bivalves of the genera *Ostrea* and *Crassostrea* of the family Ostreidae because of their economic importance, but numerous other shellfish are involved also.

The increase in importation of mollusks from other countries such as *Crassostrea gigas* Thunberg 1793, the Pacific oyster, and *Ostrea edulus* Linnaeus 1758, the European flat oyster, has resulted in introduction of new parasites and diseases into the United States. Further, transfer of these and endemic species of mollusks around the coast of North America has caused the spread of their parasites (and predators as well). The problem of importation of foreign parasites and pathogens (from other countries or regions) has become of sufficient importance to cause development of specific control procedures such as the establishment of controlled or prohibited areas and species, examination and certification, and quarantine arrangements. Of concern to science, industry, and government are the oysters mentioned above as well as the mussels *Mytilus edulus*, Linnaeus, 1758; *Brachidontes recurvis* Rafinesque, 1820; and others. Interest in the parasites and diseases of other commercially important mollusks such as *Mercenaria*

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mercenaria (Linnaeus, 1758), the hard clam or quahog; *Mya arenaria* (Linnaeus, 1758), the soft clam; *Spisula solidissima* (Dillwyn, 1817), the surf clam; *Placopecten magellanicus* (Gmelin, 1791), the ocean scallop; *Aequipecten irradians* (Lamarck, 1819), the bay scallop; and *Haliotis rufescens* Swainson, 1822, the red abalone, has grown also in the last decade due to increased interest in improved management or culture of these organisms. Consequently, most of the research is concentrated in the mollusk-producing regions of the northwestern United States (Oregon and Washington) and adjacent British Columbia, the Gulf Coast (Texas, Louisiana, Mississippi, Alabama, and Florida), the Mid-Atlantic (Virginia, Maryland, Delaware, New Jersey, and New York), the northeast (Connecticut, Rhode Island, Massachusetts, and Maine), and the nearby maritime provinces of Canada (Fig. 1). Research activity related to abalone occurs mostly in California. (A number of relevant publications are provided in the References section.)

The literature mentions a large number of symbionts (employed here in the broad sense) which infect oysters (*Ostrea* spp. and *Crassostrea* spp.) and other bivalves and cause diseases or are suspected of doing so (Appendix I). In his very useful recent publication, Sindermann (1977) listed 10 diseases of cultured oysters (*Crassostrea virginica* Gmelin, *Crassostrea gigas* Thunberg, and *Ostrea edulus* Linnaeus) in the United States and Canada and mentioned at least 6 others and there are more. The 10 primary diseases cause significant mortalities. Some of those in the "mentioned" category are merely suspected of causing disease, having been found in host tissues during surveys, but some are known to cause deaths also.

Undisturbed or relatively undisturbed natural populations of most (if not all) animals and plants bear parasites and pathogens.

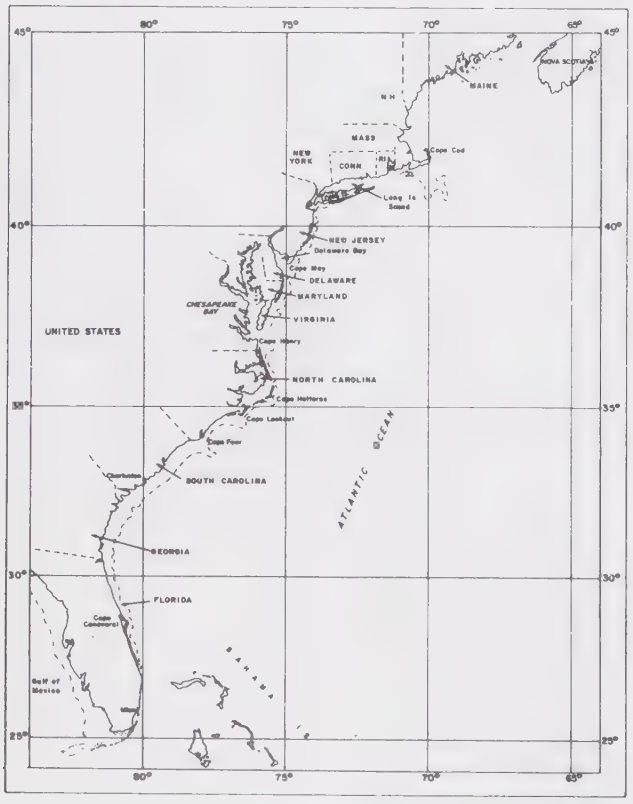

Figure 1.—East coast of the United States.

Undoubtedly, disease-related mortalities occur in such populations. When man intervenes, either by altering the environment, by moving animals and plants to new habitats or by bringing them under culture, losses due to disease increase—sometimes so drastically that epidemics or epizootics involving numerous deaths occur. At times the extensive mortalities result in severe diminishment of production and ensuing commercial losses. Animals under culture or in experimental or display aquaria, which usually are crowded, are particularly troublesome in this regard.

In North America, oysters have been widely transported and transplanted and under crude culture since the end of the last century. In recent years oyster culture techniques have become more sophisticated, though most commercial producers continue to utilize procedures developed and refined well before World War II, which involve transplantation of young oysters, called "seed-oysters" from good setting beds to "grow-out" or fattening beds whence they are harvested when they or the market are ready. As would be expected, "oyster-kills" (severe mortalities) have occurred with some frequency on all coasts of the United States and Canada where oysters are under such culture. Two such disease events are the subject of the remainder of this paper.

Mortalities of *Crassostrea virginica* Gmelin populations along the gulf and east coasts of the United States and in Canada (Fig. 1) in the late 1940's and the 1950's and later in the late 1950's and early 1960's caused interest in the parasites and pathogens of *C. virginica* and related oysters to intensify. Federal and state governments and industry became especially concerned. Since my institution, the Virginia Institute of Marine Science, was involved deeply in both efforts, they will be described as examples.

"DERMO" DISEASE OR "FUNGUS" DISEASE OF *CRASSOSTREA VIRGINICA*

When the oil industry of the Gulf of Mexico was accused by oystermen of causing deaths in natural and cultivated beds of oysters (*C. virginica*) along the U.S. coast of the Gulf of Mexico (the gulf coast) in the late 1940's, research was begun to find the possible cause or causes.

Scientists found the apicomplexan protistan *Perkinsus marinus* [Phylum Apicomplexa, Class Perkinsia, Order Perkinsida: first named *Dermocystidium marinum* and then *Labrynthomyxa marina* (which was then considered to be a fungus—hence the confusion in the common name of the disease)] to be responsible (see Appendix II). Investigations made elsewhere for the same reasons showed the organism to be present in natural and cultivated populations of oysters (*C. virginica* Gmelin) along the entire east coast of North America from Florida to Massachusetts as well as on the gulf coast (Fig. 1). From Chesapeake Bay southward and into the Gulf of Mexico, it causes mortalities of epizootic proportions; elsewhere it is mostly enzootic [except in Delaware Bay (Figs. 1, 2) in the mid-1950's when mass mortalities, apparently due to importation of infected oysters from Virginia, were reported].

The pathogen can be identified easily in prepared cultures or in squashes or sections of tissue taken from live or moribund hosts. Crude experimental infections can be brought about in the laboratory but the etiological agent has not been obtained in pure culture.

Infections can be reduced or mitigated chemically under laboratory conditions, but not eliminated. Chemical control in nature is not now possible and may never be feasible due to the dilutive and dispersive nature of the "universal" solvent and/or

carrier—water. Under farming conditions, losses can be reduced by avoiding planting seed oysters in infested high salinity areas. This salinity relationship has been demonstrated in the laboratory and in nature. As recently as 1982 the pest moved into waters from which it was previously excluded, when drought in 1980 and 1981 caused salinities in Chesapeake Bay to increase and "move" upstream. The parasite does not do well in salinities below 15 ppt. Losses can also be reduced by timing the planting and harvesting of the host. The parasite is also temperature-dependent and causes most mortalities in summer and early fall when water temperatures are between 25° and 33°C. Intensity of infection and mortalities can be reduced by controlling the density of planting, since it has been found to be density-dependent as well.

Because the pathogen, *P. marinus*, has not been isolated in pure culture, Koch's postulates have not been satisfied. Additionally, the life cycle is not completely understood and it is not known whether reservoir or intermediate hosts are required or involved but it may not require them because of its mode of sporulation and the fact that in some observations infections seem to be spread to other hosts by material from disintegrating neighbors. It forms sporangia which release biflagellate zoospores. That some related organisms have direct life cycles adds strength to the arguments of J. D. Andrews of the Virginia Institute of Marine Science and others who contend that no alternate hosts are involved. It (or closely related species) has (have) been found in many other bivalves (Appendix I).

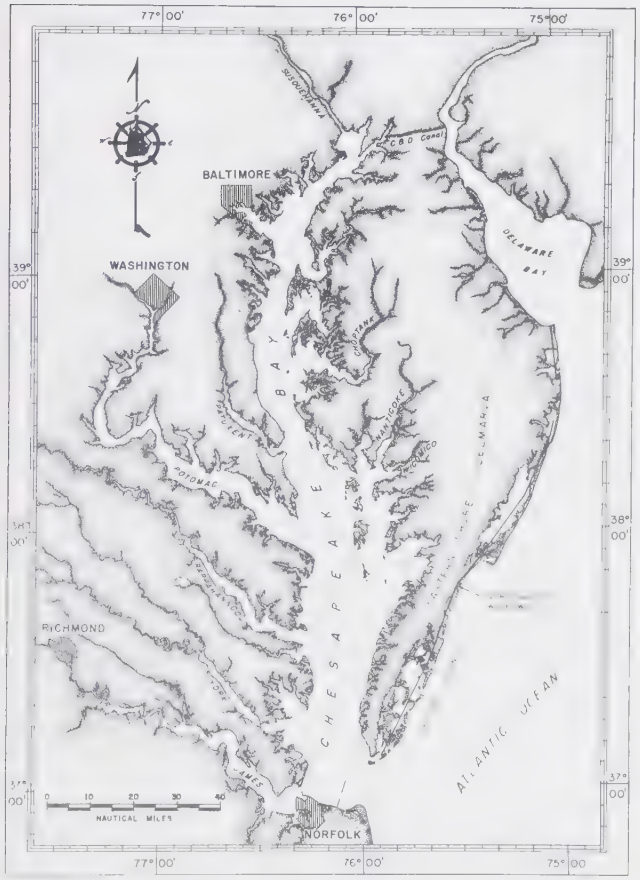

Figure 2.—Chesapeake and Delaware Bays and intervening coastal waters.

"MSX" DISEASE OR " THE DELAWARE BAY" DISEASE OF *CRASSOSTREA VIRGINICA*

In 1957, mortalities began to occur in cultivated populations of oysters (*C. virginica*) in Delaware Bay. Because of the proximity, even contiguity of Chesapeake Bay through the connecting Chesapeake and Delaware Canal and via the intervening Atlantic coastal lagoons and embayments and the associated intracoastal waterway, and because of frequent transfer of hosts between these bodies of water by fishermen, scientists anticipated infestation of the Chesapeake system (Fig. 2). Industry and government became concerned, and considerable scientific effort was mounted in the states of New Jersey (Rutgers University), Virginia (Virginia Institute of Marine Science—VIMS), and Maryland (Chesapeake Biological Laboratory at Solomons Island, Maryland—now a part of the University of Maryland Center for Environmental and Estuarine Studies).

The disease, called "MSX-disease" (for Multinucleated Spore X—a name coined before the causative agent was discovered and described), or "Delaware Bay disease," was found by epidemiological techniques to be caused by a "sporozoan" (Phylum Balanosporida, Class Stellatosporea, Order Balanosporida) parasite *Haplosporidium nelsoni* (=*Minchinia nelsoni*). See Appendix II for taxonomic placement. The pathogen was found in populations of *C. virginica* from Massachusetts to North Carolina but was most concentrated in populations in Delaware Bay and Chesapeake Bay, where it caused mortalities of from 50 to 60% annually until the commercial plantings in infested areas were killed by the pathogen or harvested by industry. In Delaware Bay (Fig. 2), oyster production dropped from about 2 million bu to about 10,000 bu annually in about 2 yr. In Virginia's Chesapeake Bay (Figs. 2, 3), it dropped from 4 million to 2 million bu/yr in a

Figure 3.—Distribution of MSX in oyster-producing regions in lower Chesapeake Bay. Areas are classified according to levels of infestation by *Haplosporidium nelsoni* (which causes MSX disease) under conditions of average salinity distribution. Type I (very dark) areas are heavily infested and oysters planted there experience significant mortalities. Oyster culture in this area must be carried out on a very cautious basis. Areas with lower infestation levels (Types II, III, and IV) are normally more productive and less troublesome, experiencing progressively fewer deaths and requiring fewer accommodations and precautions for successful oyster (*C. virginica*) culture. During prolonged drought in the upper watersheds salinity moves upstream as does MSX disease. During severe wet periods in the upper watersheds they move downstream. Prolonged drought periods cause serious mortality problems and economic losses for industry. They must be anticipated and responded to. (From Haven et al. 1978.)

similar period (1 U.S. bushel = about 35.2 l). It is still present and a threat in formerly infested regions of appropriate salinity.

Epidemiological studies indicate MSX disease to be salinity-dependent, occurring in areas ranging from 15 to 35 ppt. Figure 3 depicts the areas of infestation of lower Chesapeake Bay and the coastal lagoons of Virginia's Eastern Shore. In this figure the oyster-growing areas are classified according to level of MSX infestation occurring in years of average rainfall and salinity. These zones are used in management by accommodation or avoidance techniques. During drought years, higher salinity water moves upstream in the Bay and its tributaries and invades areas where the water was previously fresh. Since MSX is salinity-dependent, it is able to invade formerly uninfested zones or intensify where it already is, depending upon the level of saltiness of the water. It is most lethal at 20 to 25 ppt. This salinity dependence was again demonstrated forcefully in 1982 when MSX infections and associated mortalities appeared in the normally disease-free and lower salinity waters of upper Chesapeake Bay due to the drought of 1980 and 1981.

Like *P. marinus* above, it is also temperature-dependent, but not as closely so (most deaths occur in summer but some occur in late winter as infected individuals succumb to the combined stresses of over-wintering plus disease and associated poor physiological condition). First year oysters normally are not killed but older ones are.

MSX, or Delaware Bay disease, cannot be treated in the laboratory or in nature but can be avoided by not planting susceptible seed or market oysters in areas of known high infestation and by timing the planting and harvesting of oysters to avoid periods of highest mortality in areas of moderate infestation. As with Dermo-disease, chemical control is not now possible and may never be feasible. Disease resistance apparently develops in populations endemic in areas infested with the pathogen, but introduction of new susceptible hosts usually results in numerous deaths. Some investigators and institutions claim to have developed disease-resistant strains by controlled breeding techniques. Their aim in these research efforts has been to develop resistant oysters to be used as "brood-stock" to replenish populations in MSX-decimated areas.

The pathogen has not been isolated and the requirements of Koch's postulates have, therefore, not been met. The life cycle is not fully elucidated and it is not known whether intermediate hosts or reservoir hosts other than oysters are involved. As the scientific name implies, encapsulated spores are formed. Some investigators contend that no intermediate or reservoir hosts are required. Others argue that they are. It is known that organisms very much like *H. nelsoni* occur in other bivalves and in some shipworms and other crustaceans.

A similar and related disease occurs in oysters (*C. virginica*) in the coastal regions and tributaries of the Eastern Shore of Maryland and Virginia and extends northward into the waters of Long Island (Figs. 1, 2, 3). SSO disease, called thus for "seaside organism," is caused by *Haplosporidium costale* (Appendices I and II), a relative of the MSX organism, *H. nelsoni*.

Research to answer the unanswered questions mentioned above continues on both "Dermo" and "MSX" diseases of *Crassostrea virginica*. Solution of some of the critical remaining questions, especially those relating to isolation and culturing of the pathogens, explanation of the life cycle, and development of methods of mitigation, prevention, or cure, is of importance in efforts to restore oyster production in both Delaware and Chesapeake Bays.

During the course of the research on the parasites and pathogens of *Crassostrea* and *Ostrea*, species of which have been imported from the Far East and Europe and moved around between the coastal waters of North America, science has learned that diseases endemic to *Crassostrea virginica* or to a single geographical location have been transferred to other areas as industry has moved the hosts around. Additionally, parasites and diseases have been brought to North America with imports of *C. gigas* from the Far East and *O. edulus* from Europe. They have been spread around North America. Many in the United States oppose direct importation or transfer of hosts from one area to another. As indicated above, some states have taken measures to restrict importation and intrastate transfer.

In summary, studies on both of these diseases typify the thrust and status of marine invertebrate pathobiological research in the United States, which is largely devoted to examining: 1) The roles of parasites and pathogens in natural, cultivated, and captive populations of economic importance; 2) the interactions between parasites and pathogens and pollution; 3) human health aspects of invertebrate diseases; 4) the impacts on marketability of fishery products; and 5) mitigation, prevention, or treatment of diseases in experimental or economic-level culture activities. Lessons learned demonstrate forcefully that transfer of hosts and their parasites to new regions, or exposure of susceptible hosts to parasites of relatives in new regions, can be dangerous and that importation and exportation of oysters and other shellfish must be done with great care. They also emphasize the importance of an adequate knowledge of the host and its parasites and pathogens and the ability to assure good quality water in proper management of the fisheries and of aquaculture and in the maintenance of natural populations.

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APPENDIX I

A PARTIAL LIST OF IDENTIFIED DISEASES OF BIVALVE MOLLUSKS IN NORTH AMERICAN MARINE WATERS[1]

A. Viral
1. Herpes-type virus diseases
   a. Digestive gland virus disease—*Crassostrea virginica*, mortalities reported, Piscataqua River, Maine
   b. Genital tissue or ovacystis disease—*C. virginica* (Papova virus?)
   c. Digestive gland virus disease—*C. virginica* (C-type oncorona virus)
   d. Neoplasmic disease—*Mya arenaria* (uncharacterized filterable agent)
   e. Lukemic disease—*Mya arenaria* (probable virus infection)

B. Chlamydia
Chlamydial disease—*Mercenaria mercenaria*, the hard clam (digestive diverticulum—Chesapeake Bay)

C. Bacteria
1. Bacillary necrosis—*C. virginica* larvae (*Vibrio anguillarum*, *V. alginolyticus*, *Vibrio* spp., also possibly aeromonads and pseudomonads, U.S. east coast)
2. Bacillary necrosis—*Mercenaria mercenaria* larvae (same etiological agents as above, U.S. east coast)
3. Focal necrosis—*C. gigas* (unidentified gram-positive bacterium—Willapa Bay, Wash.)

D. Fungi
1. Dermo-disease—*C. virginica* (*Perkinsus marinus*—severe mortalities in waters of gulf coast and east coast, United States). Also found in *Ostrea equestris*, *O. frans*, *Mercenaria mercenaria*, *Mya arenaria*, *Argopecten irradians*, *Brachiodontus recurvis*, *Martesia* spp., and others.
2. Larval mycosis of oysters—*C. virginica* (*Sirolpidium zoophthorum*—U.S. east coast)
3. Larval mycosis of clams—*Mercenaria mercenaria* (*Sirolpidium zoopthorum*—U.S. east coast)

E. Protozoan
1. MSX disease or Delaware Bay disease—*C. virginica* (*Haplosporidium nelsoni*—U.S. east coast)
2. Seaside disease—*C. virginica* (*Haplosporidium costalis*—high salinity coastal waters extending from Chesapeake Bay mouth to Long Island Sound)
3. Hexamitiasis—*C. virginica* [*Hexamita inflata* (a flagellate)—Prince Edward Island, Canada]
4. Nematopsiasis—*C. virginica* [*Nematopsis ostrearum* (a gregarine)—Chesapeake Bay to Louisiana]

F. Metazoans
1. *Mytilicola* or red worm disease—*C. gigas* and *Ostrea lurida*—the Olympic oyster [*Mytilicola orientalis* (parasitic copepod)—U.S. west coast]. Also reported from mussels.
2. Trematodiasis—*C. virginica* [*Bucephalus haimeanus* (Digenea)—brackish waters U.S. east coast and elsewhere]

G. Diseases of unknown etiology
1. Malpeque Bay disease—*C. virginica* (causative agent unknown—Gulf of St. Lawrence, Canada)
2. Denman Island disease—*C. gigas* (agent unknown—British Columbia, Canada)

[1]Adapted from various sources, including Sindermann (1977) and Farley (1981).

APPENDIX II

CURRENT TAXONOMIC ARRANGEMENTS OF THE PROTISTAN OYSTER PARASITES DISCUSSED[1]

Subkingdom Protozoa

Phylum Apicomplexa Levine, 1970
Class Perkinsea Levine, 1978
Order Perkinsida Levine, 1978
Genus *Perkinsus* (= *Dermocystidium*, *partim*)
Perkinsus marinus (Mackin, Owen, and Collier, 1950)
(= *Dermocystidium marinum* Mackin, Owen, and Collier, 1950)

Phylym Ascetospora Sprague, 1978
Class Stellatosporea Sprague, 1978
Order Balanosporida Sprague, 1978
Genus *Haplosporidium* (= *Minchinia*, *partim*)
Haplosporidium nelsoni (Haskin, Stauber, and Mackin, 1966)
(= *Minchinia nelsoni* Haskin, Stauber, and Mackin, 1966)
Haplosporidium costalis (Wood and Andrews, 1962)
(= *Minchinia costalis* Wood and Andrews, 1962)
Order also includes the Genera *Urosporidium* and *Minchinia*

[1]Levine, N. D., J. O. Corliss, F. E. G. Cox, G. Deroux, J. Grain, B. M. Honigberg, G. F. Leedale, A. R. Loeblich III, J. Lom, D. Lynn, E. G. Merinfeld, F. G. Page, G. Poljansky, V. Sprague, J. Vavra, and F. G. Wallace. 1980. A newly revised classification of the Protozoa. J. Protozool. 27:35-58.

Some Aspects of the Biology of the Trematode, *Proctoeces maculatus*, in Connection With the Development of Mussel Farms on the Black Sea[1]

V. K. MATSHKEVSKI[2]

ABSTRACT

An extensive infection of mussels, *Mytilus gallaprovincialis* Lam., by parthenitae of the trematode *Proctoeces maculatus* Odhner, 1911 (family Fellodistomatidae Nicoll, 1913) has been recognized within the mussel farm in the southwestern region of the Black Sea (Yegorlitsky Gulf).

The life history of the above trematodes has been studied. Mussels are the first intermediate host for these helminths. Other invertebrates are supplementary hosts for *P. maculatus*. Fishes proved to be the definitive hosts for *P. maculatus*.

In studies of the biocoenotic bonds of *P. maculatus* it has been found that invasive cercariae discharged into the ambient environment are eliminated in large quantities by animals common to coastal bioceonoses.

An extensive infection of mussels (*Mytilus gallaprovincialis* Lam.) by trematode parthenitae (*Proctoeces maculatus* Odhner, 1911; family Fellodistomatidae Nicoll, 1913) was recognized within the mussel farm in the southwestern region of the Black Sea (Yegorlitsky Gulf).

The life history of this trematode has been studied and is the subject of this report. Mussels have been found to be the first intermediate host for these helminths. Development of the series of parthenogenetic sporocyst generations takes place in these hosts. Supplementary hosts for *P. maculatus* are invertebrates such as the gastropods *Rissoa splendida* and *R. membranacea* as well as the polychaete *Nereis succinea*. The cercariae develop into metacercariae within both the gastropods and the polychaetes. In some cases single large metacercariae equipped with a fully developed genital system were revealed in mussels, yet I tend to believe this to be an abnormal phenomenon. The definitive hosts for *P. maculatus* proved to be the fishes *Grenilabrus ocellatus* and *Gr. griseus*. The above-mentioned gastropods and polychaetes comprise a substantial part of the diets of these fishes.

It should be noted that *R. membranacea* and *N. succinea* were recorded as supplementary hosts for *P. maculatus* for the first time. Experimental evidence points to the fact that supplementary hosts surely participate in the life history.

When feeding the definitive hosts of these trematodes infective or invasive cercariae, I obtained evidence that they are digested within the digestive system of fishes.

In considering the potential destructiveness of *P. maculatus* in mussel farms it should be noted that among the hosts the worst infection by any particular form of *P. maculatus* is recorded in mussels (28,000 sporocysts per individual). Parthenitae infect the pallium, gonads, hepatopancreas, and other organs, comprising one-fifth (20%) of the biomass of the soft tissues in the mussels in some cases.

Infected mussels have a depressed appearance, their valves close loosely [weakly], their attachment to the substratum becomes weak, and finally they break away from the collectors. When mussels are kept in seawater deficient in oxygen those infected by the parasites perish first. Histological examination of infected and uninfected tissues shows that the damage to the tissue structures by the parthenitae results in the complete or partial castration of the host. The negative effect of sporocysts upon both the carbohydrate and lipid metabolism in Bivalvia is established.

A characteristic feature of the distribution of *P. maculatus* within the mussel population is its wide occurrence (45%) among the 2- to 3-yr-old mussels (Fig. 1) comprising the bulk of the population in the Black Sea (Vorobiev 1938; Ivanov 1968). The [deleterious] effect of the parasite upon the reproductive potential of the host is beyond doubt [question]. Experiments showed that when artificially stimulated to breed by elevated temperature, mussels are able to partially divest themselves of their parasites. Sporocysts and cercariae are ejected from the acinus of the gonads and discharged into the ambient water where they could be seen by the unaided eye. This is one of the methods of recognizing infected mussels.

In studies of the biocoenotic bonds of *P. maculatus*, it has been found that invasive cercariae discharged into the surrounding environment are ingested in large quantities by animals common to coastal biocoenoses such as: the Crustacea—*Palaemon elegans*, *P. adspersus*, *Gammarus olivii*, *Pachygrapsus marmoratus*, and *Myzidacea* gen. sp.; the polychaetae *Nereis succinea*; the molluscs—*Bittium reticulatum*, *Nana donovani*, *Rissoa splendida*, and *R. membranacea*; and the fishes—*Grenilabrus ocellatus*, *Gr. griseus*, *Neogobius melanostomum*, *N. niger*, and *Pomatoshistus microps* Leopardinus. Some of these animals participate in the life history of *P. maculatus* as intermediate or definitive hosts.

Proceeding from my own data, as well as those in the literature, I regard the trematode *P. maculatus* as a characteristic component of the coastal biocoenoses in the Black Sea where the fishes and invertebrates representing their intermediate or definitive hosts are present constantly.

Continued development of mussel farms in the Black Sea requires further studies into the biology of *P. maculatus* in order to provide information required for effective management of those sea farms.

[1] As employed here, trematode signifies Digenea.

[2] Institute of Biology of the South Seas, Ukranian Academy of Sciences, Sevastopol, U.S.S.R.

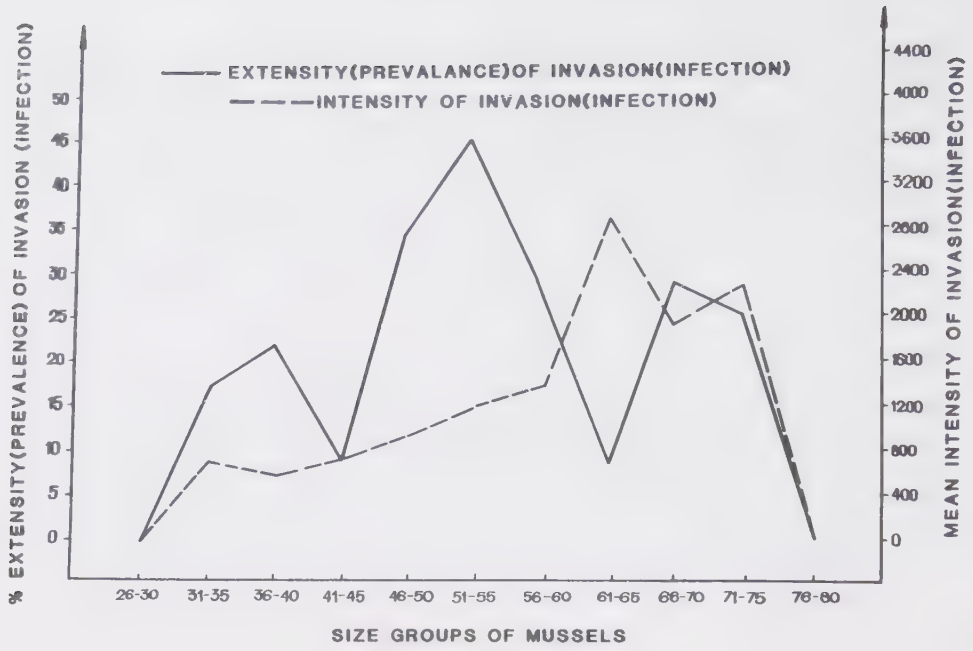

Figure 1.—Extensity and intensity of infection by size groups.

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Special Features of the Infection of the Mollusk, *Littorina rudis* (Maton, 1797), With Parthenitae of *Microphallus pygmaeus* (Levinsen, 1881) *nec* Odhner, 1905 and *M. piriformes* (Odhner, 1905) Galaktionov, 1980 (Trematoda: Microphallidae) From the White Sea[1]

K. V. GALAKTIONOV[2]

Microphallus pygmaeus and *M. piriformes* are the most common parasites in the littoral mollusk, *Littorina rudis*, in the Barents and White Seas (Galaktionov 1980). Their life cycles are characterized by the absence of free-swimming cercariae and second intermediate hosts. The common eider, *Somateria mollissima*, is the final host.

The material on which this study was based was collected from the Tchupa Bay of the Kandalaksha Gulf during the summers and autumns of 1978, 1979, and 1980. Altogether, 5,748 samples of *L. rudis* were examined. Microphallid daughter sporocysts could be subdivided into four age groups: 1) Sporocysts containing embryo balls; 2) sporocysts containing cercariae embryos; 3) sporocysts with developing metacercariae, and 4) mature sporocysts with metacercariae ready for invasion.

Infection of *L. rudis* by mature sporocysts of both *M. pygmaeus* and *M. piriformes* is relatively constant during the entire summer. The high infection extensivity [prevalence] seen in June is probably related to migration of healthy mollusks into the sublittoral zone. The development of the parasites within littorines infected in autumn of the preceding year is fully completed by July or August. The common eider appears in the region of the Kandalaksha Gulf in May and begins occupying the Islands [off the coast of the continental land mass] for nesting even when they are still covered with snow. The littoral zone is also still ice-coated, which makes a spring invasion of mollusks practically impossible. Owing to this fact the percentage of littorines infected with young parthenitae in summer is very low. Mass invasion of the White Sea *L. rudis* with both *M. pygmaeus* and *M. piriformes* occurs in July when the first broods of eider are encountered. Since young broods remain together near the nesting places, mollusks infected with sporocysts containing embryo balls are found only on the islands in the open sea in September. In November, littorines infected with young parthenitae are found everywhere. In autumn, when weather conditions are worsening, the mortality of mollusks increases. Those with severe infections of the inner organs die first. Because of this, a decrease in extensivity [prevalence] of *L. rudis* invasion [infection] with mature microphallid parthenites was observed in autumn.

The extensivity [prevalence] of infection of *L. rudis* with parthenitae of *M. piriformes* increases from the coastlines of the open sea islands towards the emergent continental masses. I observed a reverse tendency in the process of littorine infection with sporocysts of *M. pygmaeus*.

It seems obvious that the greater number of mollusks infected with mature parthenitae of *M. piriformes* successfully survive cold months due to favorable littoral ice-regime conditions in the continental bays. The effect produced by this type of parasite on the inner organs of the littorine is relatively insignificant. The principal loss occurs in littorines infected by mature parthenitae of *M. pygmaeus*, which cause complete liver and gonad destruction in the mollusk.

Because of the instability of the ice cover, living conditions around the off-lying islands are extremely inclement during cold months. The selective advantages that are characteristic of mollusks infected with *M. piriformes* compared with those infected by *M. pygmaeus* apparently seem not to be realized [in the waters around the islands], and the great majority of littorines containing both types of mature parthenitae is lost during winter. Thus, infection with *M. piriformes* among the littoral population of *L. rudis* from the continental bays is accumulated from year to year. Indeed, the percentage of littorines infected with this parasite reaches values as high as 80 to 90%. Moreover, specimens of older age groups are heavily infected. And since microphallid parthenitae cause parasitic castration of mollusks, the maintenance of *L. rudis* populations here depends exclusively on females breeding for the first time and upon migration of littorines from neighboring populations.

[1]No Literature Cited section was supplied by the author.

[2]Murmansk Marine Biological Institute, Murmansk, U.S.S.R.

The Helminth Fauna and Host-Parasite Relations of Squids *Sthenoteuthis oualaniensis* (Lesson) (Cephalopoda, Ommastrephidae) in the Indian Ocean and the Red Sea

N. N. NAIDENOVA, C. M. NIGMATULLIN, and A. V. GAEVSKAYA[1]

ABSTRACT

Nine species of helminths, including two species of trematodes, three of cestodes, two of nematodes, and one species of acanthocephalans, were found in the squid, *Sthenoteuthis oualaniensis*, from the Indian Ocean and the Red Sea. According to the incidence of infection and the degree of density of the parasite-host relationships, all of the helminths were distributed into three groups: Main, secondary, and accidental helminths [parasites]. The age and geographic changes of the helminth fauna of *S. oualaniensis* are presented. The significance of *S. oualaniensis* in the life cycle of helminths is discussed. The helminth fauna of the squids *S. oualaniensis* and *S. pteropus* from the Atlantic Ocean is compared. The principle resemblance of the helminth fauna of these species of squids is revealed. The possible reasons for the reduced diversity of species of helminths of *S. oualaniensis* are discussed.

INTRODUCTION

Many reports on the important role of squids in the life cycles of different systematic groups of helminths have been published recently (Gaevskaya and Nigmatullin 1975; Naidenova and Zuev 1978; Hochberg 1975; Stunkard 1977; and others).

In the eupelagic of the tropic zone of the World Ocean two species of the genus *Sthenoteuthis*—Atlantic *S. pteropus* (Steenstrump, 1855) and the Indo-Pacific *S. oualaniensis* (Lesson, 1830)—dominate the squids in terms of mass (numbers) and size. The role of the first species in the parasite fauna of the eupelagic of the Atlantic Ocean has been studied relatively well, but we have only fragmentary information about the helminth fauna of *S. oualaniensis*.

In this report we describe the results of a quantitative and qualitative study of the helminth fauna of *S. oualaniensis* in the tropical parts of the Indian Ocean and (partially) of the Red Sea.

The distributional area of *S. oualaniensis* includes the Indo-Pacific region from the west coast of Central and South America to the Cape of Good Hope and from Japan to northern Australia. Its numbers are dominant among the nektonic predators—consumers of the III to IV orders. The mantle length reaches 45 cm, but specimens larger than 25 cm are very rare. Males are smaller than females; their maximum length is 24.5 cm.

Considering certain morphophysiological and ecological features there are two well-differentiated forms within the species—a small early spawning form and a large late spawning one (the A and B forms mentioned in foreign literature) (Clarke 1966 and Nesis 1977).

According to our data the food links of these squids are various and change essentially in ontogenesis. The main food of young, 8 to 10 cm long, squids are large copepods, euphausiids, amphipods, young decapod crustaceans, chaetognaths, and fish larvae. The role of crustaceans in their food is reduced as the squids grow, and those > 13 to 15 cm long eat pelagic, open-ocean fish almost solely (Myctophidae in 60 to 80% of the cases) as well as small species and juvenile forms of squids—often of their own species. Sometimes they eat large crustaceans such as shrimps and blue swimming-crabs. At the same time mesoplanktonic organisms (copepods, amphipods, ostracods, chaetognaths, and others) are usual in the stomachs of even the largest squids. They are devoured with the main food organisms—Myctophidae. The food spectrums of the representatives of small and large forms are similar.

In their turn young squids serve as general food for many kinds of marine birds, dolphin fishes, snake mackerels, and lancetfishes. Middle-sized and large squids are eaten by yellowfin, longfin, and bluefin tunas; marlins; sailfishes; whitetip sharks; cachalots; and dolphins (Wormuth 1976; Young 1975; and our data). Thereby, *S. oualaniensis* is an important intermediate link between macroplankton and small fishes in the trophic structure of the eupelagic zone—planktophages on the one side and large predatory teleost fishes, sharks, marine mammals, and birds on the other side.

Our materials were taken in the tropical zone of the Indian Ocean and the Red Sea between May and August of 1978. Three hundred and thirty-seven squids were examined on board the ship *Professor Vodyanitsky*.

QUALITIES OF THE HELMINTH FAUNA

Examination of the squids disclosed nine species of helminths—trematodes [digeneids], cestodes, nematodes, and acanthocephalans.

About 2,000 metacercariae of Didymozoidae gen. and sp. were found in oval cysts with thin, transparent envelopes. They are located mainly in the external coverings of the stomach and less frequently in its muscular layer or caecum covers. The most compact accumulations of cysts were found in the forepart of the stomach, usually near a general [principal] blood vessel. From there they spread to the rest of its surface. Worms move in their

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cysts. The fact that upon fixation some larvae have long narrow bodies and others have wide flattened ones demonstrates this feature.

Judging from the morphology of the metacercariae they are of the *Monilicacecum* type, with a large muscular stomach situated above the level of the ventral sucker. The oral sucker is small. The pharynx is rather powerful and muscular. The acetabular sucker is small. The larvae differ by size and number of chambers per caecum. It should be noted that only large forms are registered [recorded] as being in the internal muscular layer of the stomach. Judging from the sizes of the metacercariae, they grow inside the squid. Upon reaching the maximum size, metacercariae live for a short time and perish, after which the cover of the cyst dissolves completely and the larvae become macerated. The same phenomenon was observed in didymozoid metacercaria from *S. pteropus* of the Atlantic. It usually occurs when the squid's mantle reaches 20 cm in length and the age is from about 6 to 8 mo. Since the beginning of mass infection occurs in 2- to 3-mo-old squids, the duration of metacercarial life in the squid does not exceed 4 to 6 mo.

Didymozoid metacercariae use a wide variety of hosts, such as different plankton organisms (i.e., copepods, euphausiids, and chaetognaths) and small teleost fish (Madhavi 1968; Reimer 1971; Overstreet and Hochberg 1975; Gaevskaya and Nigmatullin 1977). High indices of infection in the squid reflect the high intensity of feeding. According to our data, the daily diet of young squid constitutes 10 to 15% of the body mass and 4 to 5% of the body mass of adults.

At the same time, didymozoid cercariae are noted as independent components of the plankton. Carried by water currents into the mantle cavity of squids, these cercariae can actively penetrate into the squid through its coelomic coverings.

The enormous infection of squid by didymozoid metacercariae indicates an important role of squids in the life cycle of these trematodes. Heavy infection of the squids is a cause of the high infection of the final fish hosts, mainly tunas, scombroids, and xiphoids. In the Indian Ocean around 100% of wahoo and 50% of the tunas are infected by the adult stages of didymozoids, with an intensity of about 100 cysts/fish (Nikolaeva and Dubina 1978).

Immature stages of the trematode [digeneid] *Hirundinella ventricosa* are encountered singly in the coelomic cavities of squids. Large specimens, with the characteristic narrowing of the body behind the acetabular sucker, have pointed body extremities. Average dimensions of the trematodes are 6.5 × 1.5 mm. The oral sucker is 0.55 × 0.72 mm, the pharynx is 0.39 × 0.40 mm, and the acetabular sucker is 1.5 mm in diameter. The morphological characteristics of these trematodes are similar to those occurring in Atlantic squids.

Upon attaining large size, cercariae of azygiat trematodes enter into the plankton and can infect squid. They occur in the host's digestive organs with ingested food. The final hosts of *H. ventricosa* are predatory teleosts—dolphins and scombroids.

Larval *Nybelinia lingualis* (Cuvier, 1817)—the plerocercoids—localize in intestinal mesenteries, on the ovary, and on the external coverings of the stomach. They encyst also in the stomach. The scolex length is 1.6 to 1.65 mm; the bothrium portion is 0.94 to 1.1 mm long and 1.4 mm wide; the tentacular sheath is 0.52 to 0.55 mm long. Dimensions of the tentacular bulbs are 0.286 to 0.319 × 0.11 mm.

Nybelinia larvae are widely spread among teleost fishes of the World Ocean. Twelve species of cephalopods have them in the Atlantic and Pacific Oceans (Kurochkin 1972; Brown and Threlfall 1968; Dollfus 1964; and others). Dollfus (1967) discovered free-living *Nybelinia* larvae to be an organic [a regular] part of the plankton.

Indices of infection of squid by *Nybelinia* exceed those of the fishes. Thus, the extensiveness of the infection of squid reaches 90%. More than 200 plerocercoids may be found in one squid. In contrast, infection of fish seldom exceeds 40% and the intensity of infection constitutes 1 to 30 plerocercoids as a rule.

Probably, the squids acquire these parasites while ingesting their intermediate hosts—copepods and euphausiids, etc. However, considering the magnitude of the alteration of infection the second intermediate hosts—small teleost fishes—become the main source of infection. The latter circumstance promotes a second accumulation of *Nybelinia* plerocercoids in squids.

The final hosts of *Nybelinia* are large active sharks of the families Carcharhinidae, Isuridae, and others, which can ingest squids both alive and dead (after the period of spawning). In the life cycle of *Nybelinia*, the squid *S. oualaniensis* is an insert host [and may be a reservoir host] between small teleost fishes and selachians.

Larval *Tentacularia coryphaenae* Bosc, 1802 are registered [recorded] for the first time as parasites of squids of the Indian Ocean with 65% infection. Large (3.0 to 8.3 mm), mobile plerocercoids locate in the internal organs and the mantle cavity, especially in its posterior end. Plerocercoids can actively embed in the mantle wall of the squids. They are widely dispersed on marine teleosts and are recorded in four species of cephalopods of the Atlantic Ocean. The final hosts of these cestodes are sharks. The first intermediate hosts are planktonic crustaceans and the second are teleost fishes. Plerocercoids infect the squids when ingested by them.

Phyllobothrium sp. larvae, encountered rarely, usually locate in the caecum, more often in the rectum. After the squid die they can actively migrate into different portions of the body. The average length of the plerocercoids reaches 5 mm, the maximum width—1.2 mm, the apical sucker—0.143 to 0.176 mm in diameter. The dimensions of the lateral suckers are 0.275 to 0.297 × 0.352 mm. The bothridia are heart-shaped and measure 0.55 × 0.72 mm.

Plerocercoids of the genus *Phyllobothrium* are rather widely dispersed in the squids of the Atlantic Ocean (Stunkard 1977; Gaevskaya 1976; and others). As the work of American scientists (Brown and Threlfall 1968) showed, infection of the squids by plerocercoids experiences monthly and yearly variation. It is apparently connected with the short (1 yr) life cycle of these squids.

In the life cycles of the phyllobothriums, *S. oualaniensis* assumes the role of insert host [another host which is inserted] between small teleost fishes and squids and the final hosts—sharks.

Two types of *Porrocaecum* sp. larvae are recorded in 24 to 57 % of squids with an intensiveness of infection of 1 to 100 specimens. They are situated in connective tissue capsules in the body cavity. Small larvae (3 to 5 mm) localize on the external wall of the stomach; large ones (20 to 25 mm) on the internal mantle wall. Adentic nematodes were found also in squids of the Atlantic Ocean, but their infection was considerably higher (96%). It may be supposed that both forms are successive stages of the development of a single species of nematode, since their morphology is similar. However, the absence of transitional forms between the small and large larvae causes bewilderment.

The life cycle of *Porrocaecum* sp. is probably as follows: The first intermediate hosts are planktonic crustaceans (euphausiids), the second are teleost fishes, the third are squids, and the final

hosts are mammals. It should be noted that *Porrocaecum caballero*, whose morphological features coincide with those of larvae registered [recorded] on the squids, has been described from *Makaira mitsukuri* from Mexican waters.

Anisakis sp. larvae are encountered relatively rarely (0.9 to 3.8%) with a low intensity of infection (one to two specimens). They locate in the ovary and coelomic membranes of the sexual cavity, rarely on the caecum walls. Ending their development in marine mammals, the larvae show great activity at high temperatures and retain their vitality for a long time. The life cycles of these larvae and the position the squids occupy in them are similar to those of the *Porrocaecum* species.

The Acanthocephala gen. and sp. I are very long and threadlike. They are found in sections of the pericardial coelom and usually attached to the mantle wall or liver with their probosces. Live worms measure from 10 to 20 cm. The morphometric characters of these acanthocephalans conform to those described from the squids of the Atlantic Ocean by Naidenova and Zuev (1978). Two mature females were found near Sokotra Island in 1964. Our most recent finds represent immature forms.

Acanthocephala gen. and sp. II were twice found in the stomach cavity of the large squids. They measured 1.0 to 1.3 cm. Their systematic identity was not determined because of poor preservation.

QUANTITATIVE INDICES OF INFECTION AND THEIR CHANGES

The total infection of the squids we examined was 98.4%. Eighty to 84% of the juveniles 2 to 8 cm long are infected with helminths. The extensiveness [prevalence] of infection of the larger squids is 100%.

According to the indices of extensiveness [prevalence] and intensity of infection, and the degree of narrowness of host-parasite relations of the squid, we may divide the helminths discovered into three groups: 1) Principal helminths (occurring at an extensiveness [prevalence] of infection of from 30 to 95% and an intensity from a few specimens to tens of hundreds of specimens)—metacercarial didymozoidae, *Porrocaecum* larvae, *Nybelinia*, and *Tentacularia*. 2) Secondary helminths (2.5 to 3.5%, single specimens)—cavital Acanthocephala gen. and sp. I, *Phyllobothrium* larvae, *Anisakis* larvae, and *H. ventricosa*. 3) Causal helminths (< 1%)—small Acanthocephala gen. and sp. II from the stomach.

As the size of the squids increases, infection by various species of helminths changes unequally [disproportionately]. The poorest is the qualitative composition of helminths of the youngest squids 2 to 4 cm long. Only metacercarial didymozoidae have been found in them. Specimens of the next size group (4 to 12 cm) have *Nybelinia* larvae in addition. As squids attain a mantle size of 12 to 14 cm in length they have all species of helminths. From then on only an increase of infection by the principal species of helminths occurs. Three types of size-age dynamics of squid infection may be identified: 1) The first type is characteristic of the largest mass of parasites—the didymozoidae. The indices of extensiveness [prevalence] of infection are large for the squids of all size groups and are approximately at the same level (80.0 to 98.7). Only the intensity of infection changes noticeably. 2) In the second type, the change of infection by the other principal helminths—*Porroceacum*, *Nybelinia*, and *Tentacularia* larvae—occurs. These parasites appear in squids 8 to 10 cm long, and when they are 14 to 18 cm long the indices of infection increase almost to the maximum. The secondary helminths—*Anisakis* and *Phyllobothrium* larvae—join this type. But the sharp rise of infection by these parasites takes place later, when the squids attain more than 20 to 22 cm in length. 3) In contradistinction to the other helminths, *H. ventricosa* and cavital acanthocephalans begin to infect specimens 10 to 12 cm long and maintain an essentially low level of infection index as the squids grow.

Infection by Didymozoidae occurs thanks to copepods, euphausiids, and chaetognaths—the principal food of the smallest squids. Further accumulation of these trematodes probably occurs when these invertebrates get into the stomachs of the squid. On the whole the formation of the helminth fauna coincides with the squid's attainment of adulthood when they become 10 to 14 cm long. This takes place when the adult squid begin to feed on adult specimens of small fishes and small squids, which are the suppliers [carriers] of cestodes, nematodes, trematodes, *H. ventricosa*, and probably of small acanthocephalans, as their principal source of nourishment. To judge from the special features of the size-age metamorphosis of the squid's infection, the majority of helminth species get into them with the representatives of different groups of fishes and small squids or with different age stages of one or another food object.

When comparing the qualities of helminth fauna and the indices of the early spawning and late spawning squids as a whole [all together], their main similarity is discovered. Their difference consists of a poorer species composition (five to nine) and low indices of infections of the early spawning forms by almost all helminths, with the exception of didymozoidae and *Nybelinia*. At the same time, all species of helminths found in early maturing squids are common for both forms, and the indices of infection of representatives of early and late maturing forms on the whole are connected with the difference of their dimensions (the length of early maturing specimens in our collections did not exceed 12.7 cm) and, in the end, of the length of life and food composition.

Within the late maturing forms the structure of the helminth fauna and the squid's infection may vary considerably depending on the geographical region of the research. In this respect the Red Sea region stands out for the paucity of its helminth fauna. It has only three species. Perhaps this is connected to an insufficient sample of squids examined from a single station. However, we do not exclude the possibility that the results obtained reflect the true situation only partially and may be a consequence of a scarcity of final hosts of the squid helminths. The high indices of infection of Red Sea squids by *Nybelinia* and the low indices of infection by didymozoidae attracted our attention.

DISCUSSION

We discovered that the chief factor leading to the infection of squids by helminths is food. As the ontogenesis of food links occurs, the helminth fauna and quantitative indices of infection also changes. The food factor promotes the transmission of these helminths to the final hosts. Xiphoid fishes, sharks, and [marine] mammals mainly use the most heavily infected medium- and large-sized squid. The latter become most accessible after spawning. Small and medium *S. oualaniensis* occur at the same time as large squids in the food of the tunas. Therefore, in this case we have full accordance between trophic and parasitic links.

Except for acanthocephalans and juvenile *H. ventricosa*, all helminths parasitizing squids represent larval forms. They have very wide [broad] specificity and use various invertebrates, teleost fishes, and squids at the same stages of their life cycles. Therefore, the use of other squids for food is the cause of the secondary accumulation of didymozoidae and different species of nematodes and cestodes in the squid. With the increase of age and size and

transition to a higher trophic level, the number grows. In the life cycles of didymozoidae, cestodes, and nematodes, there is an insert host between the second intermediate hosts—planktonic invertebrates and micronekton (i.e., fish-planktophytes and small squids), and the final hosts—large nektonic predators, occupying the top of the food chains of the eupelagic zone. To speak of the squid's position in the life cycle of acanthocephalans at present would be premature. We may only suppose that the squids are their final hosts.

Considering the high indices of infection, which are not encountered in other hosts of these helminths, the high quantity, wide dispersion, and the variety and stability of trophic links we may consider *S. oualaniensis* to be one of the main obligatory hosts for didymozoidae, *Nybelinia*, *Tentacularia*, and *Porrocaecum*. *Stenotheuthis oualaniensis* is the vehicle for their transmission to the final hosts. Wide [broad] specificity and the "fish" larvae "aspect" of the helminth fauna of *S. oualaniensis* shows it to have been "acquired" by the squids relatively recently. The parasites have successfully acclimated and are incorporating this species of host, which occupies a key position in the pathway of circulation of helminths among oceanic pelagic communities [into their circle of hosts]. At present we find different species of helminths in different stages of forming parasite-host relationships. They are strongly expressed in didymozoidae, *Porrocaecum*, *Nybelinia*, *Phyllobothrium*, and *Tentacularia*. Though the food linkages of young squids are very close to marine birds, larvae of bird parasites are absent in squids.

The helminth fauna of *S. oualaniensis* represents (as a matter of fact) an impoverished version of that in the Atlantic vicariate of *S. oualaniensis*, i.e., 8 species as compared with 15. Moreover, the first species has no helminth which does not occur in the second one. The impoverishment of the species of their parasite fauna occurs primarily because of the disappearance [or lack] of the secondary and casual species of helminths.

At times the difference in the infection indices of the common species of helminths tends toward the side of a larger quantity in *S. pteropus*. In our opinion the causes of the main differences are related to the difference in the number of individuals examined (303 specimens of *S. oualaniensis* as compared with 2,200 specimens of *S. pteropus*) and in the dimension of the squids (*S. pteropus* are 2 to 50 cm in length with a mode of 20 to 30 cm). It naturally depends on the presence or absence of the secondary and, especially, of the casual species of helminths and the degree of accumulation of the principal helminths.

The main conclusion of this comparison is that both geographic vicariates have a similar position in respect to the parasite fauna of conformable [comparable?] associations of the tropical eupelagic. This is more indirect evidence that their econiches are almost identical, though that of *S. pteropus* is somewhat wider, due to its larger size.

The ancestor of *S. oualaniensis* penetrated into the Indo-Pacific from the Atlantic Ocean, rounding the southern extremity of Africa during one of the warming Pleistocene periods. During the ensuing drop in temperature and upon isolation two allopatric species were formed. Undoubtedly, the squids themselves could not have carried the helminths from the Atlantic to the Indo-Pacific, since they were only the intermediate hosts. Considering that these geographic vicariates occupy similar econiches in homologous associations of the World Ocean and considering their high ecological valency, the formation of the helminth fauna of both species evidently proceeded simultaneously.

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Some Parasitological Aspects of Shrimp Culture in the United States

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ABSTRACT

Penaeid shrimps are presently being reared commercially in the United States and elsewhere. Parasites and diseases, however, continue to be a problem in most rearing facilities. Viruses, algae, bacteria, fungi, ciliates, microsporidans, digeneans, cestodes, nematodes, and miscellaneous conditions include representatives that have an effect on aquaculture, influence hosts in their natural environment, and produce potential public health problems.

INTRODUCTION

Commercial culture of marine crustaceans in the United States of America or by U.S. companies abroad is primarily confined to penaeid shrimps. Additionally, some facilities rear the blue crab, *Callinectes sapidus*, for the soft-shelled seafood industry; American lobster, *Homarus americanus*, and "freshwater" shrimps (*Macrobrachium* spp.) for human consumption; and various crustaceans belonging to different orders for research purposes. This paper is concerned primarily with infections of penaeids.

Many of the problems of hatching and rearing penaeid species have been solved and some penaeid species can be profitably cultured (e.g., *Penaeus stylirostris*, *P. vannamei*, *P. setiferus*, *P. aztecus*, *P. duorarum*, and *P. japonicus*). Some of the successful facilities are in the U.S. and others are in Central and South America as joint ventures with U.S. companies. As an example of the potential value of shrimp from ponds, Texas A&M University, jointly with Central Power and Light Company of Corpus Christi, Tex., has a hatchery that can produce 3 to 4 million larval shrimp per day or enough to stock 10 to 13 ha (1 ha = 0.4047 acre) of "grow-out" ponds per day. A spokesman for that operation, basing the wholesale value of shrimp at $4.40/kg for entire shrimp, estimated a return of $1,620 worth of shrimp per hectare for $325 to $400/ha invested in operational costs for a farm having 405 ha (Rosenberry 1980a, b). Ralston Purina has a large hatchery in Crystal River, Fla., as well as productive ponds in Panama. Productive ponds in Ecuador have been estimated as occupying 40,500 to 77,000 ha, with applications received by the Ecuadorian government for 58,300 ha more and one prediction of 485,800 ha of ponds by 1985 (Rosenberry 1981a). In 1980, 9,435,000 kg of penaeids were farmed in Ecuador at a value of $66 million. Some farmers obtained about 500 to 700 kg/ha per yr (1 kg/ha = 1.12 lb/acre) in two crops, whereas serious farmers obtained over 2,000 kg/ha per yr in three crops with initial investments of about $500 to $800/ha (Rosenberry 1981b). Companies from the United States and elsewhere are becoming involved in these projects and in hatcheries providing young shrimp for them. Facilities other than ponds are also extremely productive. Coca-Cola, F. H. Prince, the University of Arizona, and the University of Sonora collectively developed a flow-through raceway system in Mexico. A similar system is now producing shrimp in Hawaii, matching production of about 62,500 kg of shrimp abdomens per ha (Lightner[2]).

Control of parasites and diseases in shrimps still constitutes a significant obstacle to maintaining a continual, profitable production of these seafood products. In this report, I discuss some diseases affecting penaeids and briefly relate them to aquaculture, the natural environment, or potential public health problems. Usually, but not always, disease conditions and mortality are related to poor water quality in culture facilities.

VIRUSES

Each year additional undescribed viruses are discovered from crustaceans. A few have been shown to cause disease and death in cultured hosts. One conspicuous species from penaeids, *Baculovirus penaei*, infects the nuclei of hepatopancreatic cells. Refractile polyhedral inclusion bodies (PIB's) containing rod-shaped, deoxyribonucleic acid-virions located within the enlarged host nuclei make some infections detectable using a light microscope (Fig. 1). Stress, caused both by crowding shrimp in culture facilities and by contaminating them with specific toxicants (e.g., the polychlorinated biphenyl Aroclor 1254[3]), has increased the prevalence of PIB's in shrimp. Examination of individuals from a massive mortality of larval and postlarval brown shrimp, however, indicated that an internal ciliate (*Parauronema* sp.) and flagellate (?*Leptomonas* sp.) concurrent with the virus may have contributed to the deaths which occurred (Couch 1978).

ALGAE

Few observations have associated algae with shrimp health, but blue-green algae can grow on gills (e.g., *Schizothrix calcicola* reported by Overstreet 1973) and apparently their toxins can cause disease. Recently, *S. calcicola* and another filamentous blue-green alga (*Spirulina subsalsa*) have been implicated in hemocytic

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[2]D. V. Lightner, Environmental Research Laboratory, University of Arizona, Tucson International Airport, Tucson, AZ 85706-6985, pers. commun. December 1980.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

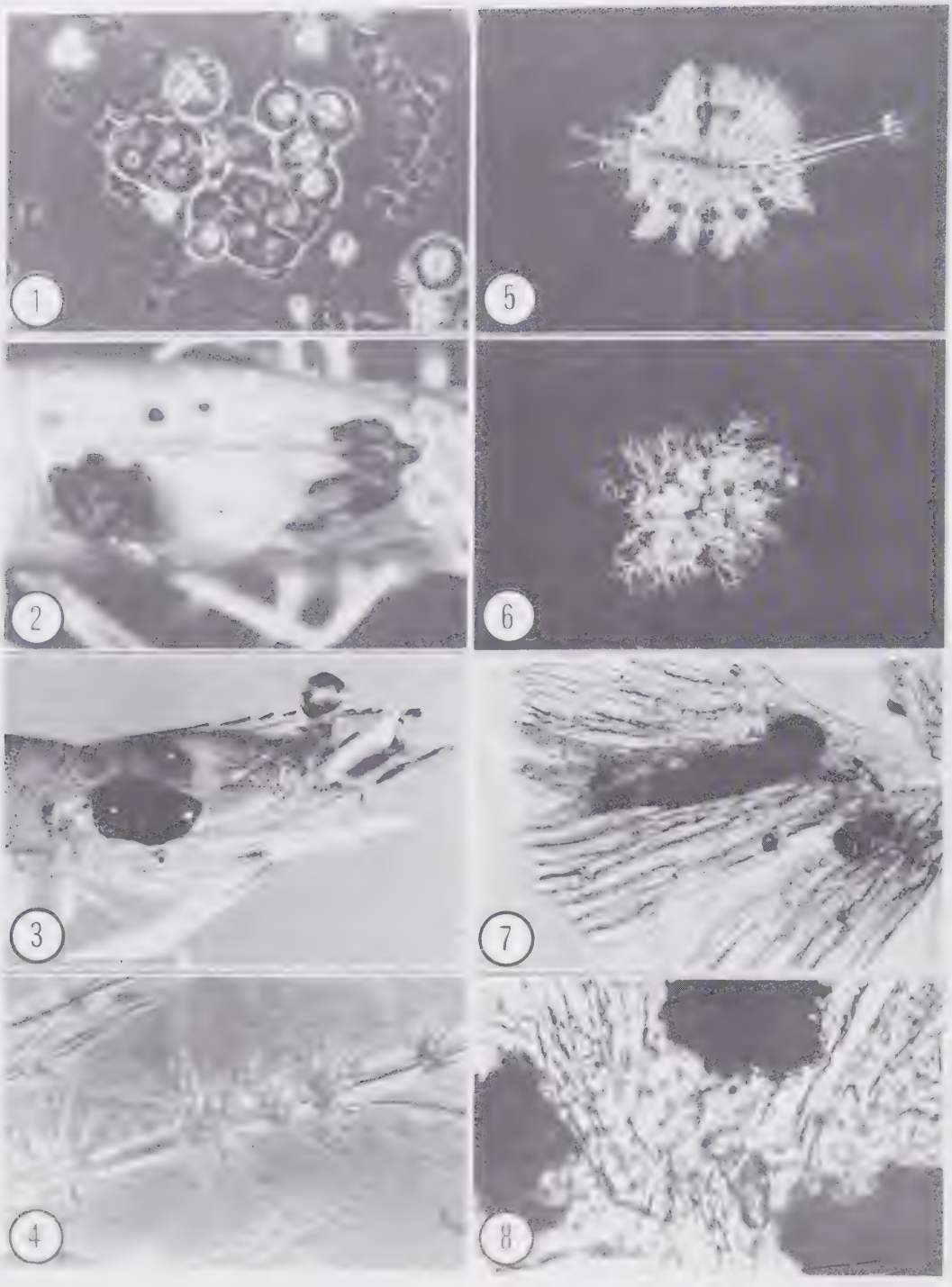

Figure 1.—Refractile tetrahedral inclusion bodies containing *Baculovirus penaei*. In hepatopancreatic nuclei of penaeid shrimp, as well as free because of fresh squash technique (from Overstreet 1978, taken by J. A. Couch).

Figure 2.—*Penaeus aztecus* exhibiting chitinoclastic "shell disease" in carapace (from Cook and Lofton 1973).

Figure 3.—"Black nodule disease" of presumed bacterial etiology in a reared specimen of *Penaeus setiferus* (from Overstreet 1983).

Figures 4 to 6.—*Leucothrix mucor* from *Artemia salina*. 4. Rosettes on seta. 5. Moderately infested brine shrimp. 6. Sloughed mat of bacterium and associated debris (all from Solangi et al. 1979).

Figures 7 and 8.—Apostome ciliate in *Penaeus aztecus*. 7. "Black gill" syndrome resulting from melanin deposition. The causative ciliate is only one of several organisms or conditions that can cause the syndrome. 8. Close-up showing organism (both from Overstreet 1978).

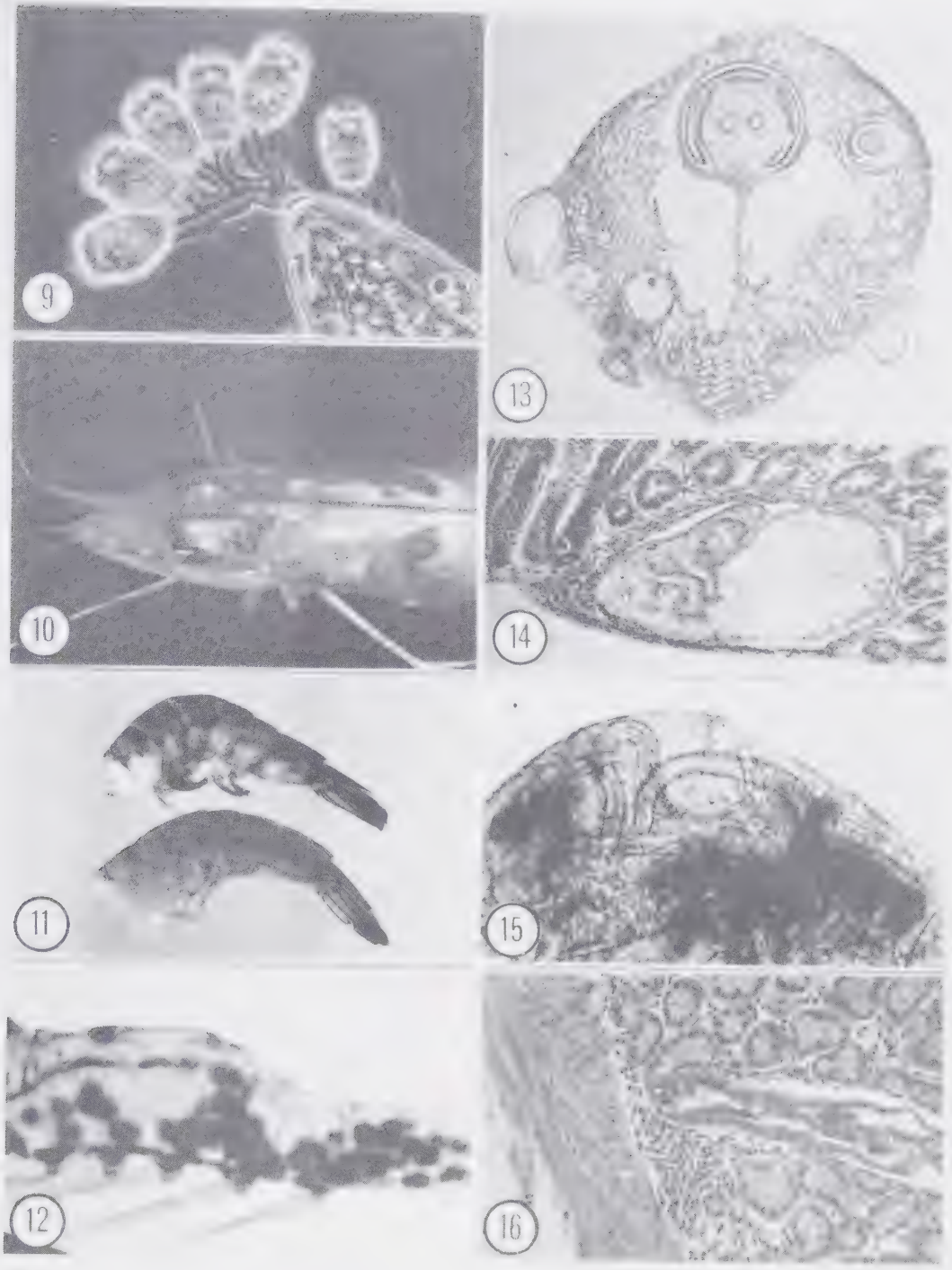

Figure 9.—A small colony of the peritrich *Zoothamnium* sp. on tip of penaeid gill filament (from Overstreet 1978; Foster et al. 1978).

Figure 10.—The microsporidan *Agmasoma penaei* infecting cells lining the circulatory system of *Penaeus setiferus* (from Overstreet 1978).

Figure 11.—Abdomens of *Penaeus aztecus*. Top specimen is infected by the microsporidan *Ameson nelsoni* and the bottom one is uninfected control. Spores surround and eventually replace the muscle bundles, resulting in "cotton shrimp disease" (from Overstreet 1978).

Figure 12.—Young shrimp with experimental infection of *Microphallus turgidus* metacercariae (from Overstreet 1978).

Figures 13 and 14.—Metacestode of tetrarhynchidean *Prochristianella hispida* in *Penaeus setiferus*. 13. Five individuals under capsular lining and embedded in the hepatopanceas proper (from Overstreet 1983). 14. Individual showing four characteristic inverted, armed tentacles within scolex.

Figure 15.—At least three developing individuals of the second stage larva of *Hysterothylacium relinquens* in hemocoel of the harpacticoid *Tigriopus californicus* (from Overstreet 1983). The third stage larva commonly infects penaeids.

Figure 16.—Larval *Hysterothylacium* type MB migrating toward muscularis mucosae in stomach of rhesus monkey 1.5 h after being administered. Note numerous surrounding eosinophils (from Overstreet and Meyer 1981).

enteritis (HE) in shrimp cultured with algae as a means of maintaining an adequate oxygen level and water quality as well as providing supplemental food and vitamins (Lightner 1978; Rosenberry 1981b). Medicated food helped reduce mortalities from secondary bacterial infections, and Lightner plans to test methods of immunizing postlarval or early juvenile shrimp to HE by feeding them killed cultures of the algae.

Other algae in shrimps, such as a diatom in the hemocoel (Overstreet and Safford 1980) and algae in muscle tissue, have been observed, but probably have little detrimental influence on entire stocks.

BACTERIA

Several bacteria have been implicated as causes of mortalities of shrimps, especially of juveniles. Major contributors to bacterial septicemia in at least *Penaeus aztecus*, *P. setiferus*, and *P. duorarum* are *Vibrio anguillarum*, *V. parahaemolyticus*, and *V. alginolyticus* (the latter is also considered *V. parahaemolyticus* biotype *alginolyticus*). Lightner and Lewis (1975) discussed various aspects of bacterial septicemia in penaeids. Moreover, in humans, *V. parahaemolyticus* can cause gastroenteritis and *V. alginolyticus* can cause inner ear and wound infections. Other bacteria of no public health import have been isolated from diseased shrimp tissue. This includes the cuticle which may be infected by a variety of chitinoclastic bacteria and fungi. Cook and Lofton (1973), however, found that *Beneckea* type I only was common to different crustaceans exhibiting black-spot, or shell-disease (Fig. 2). This aesthetically displeasing disease is most serious in crowded shrimp maintained at about 30°C and in some cases causes mortalities. Other conditions—including "black nodule disease" that affects penaeids (Fig. 3), *Macrobrachium* spp., and other shrimps—probably have a bacterial cause, even though Koch's postulates have not been satisfied for many of them.

Vaccines may prove useful for preventing bacterial diseases in penaeids. Preliminary studies exposing juvenile penaeids to autoclaved *V. anguillarum* by Lewis (1981) suggest the shrimp's immune system has humoral components that provide an immediate, short-lived response to an agent and cellular components that play a role in long-term protection.

Larval penaeids and many other crustaceans are susceptible to filamentous bacteria such as *Leucothrix mucor*. A strain of this bacterium from the brine shrimp, *Artemia salina*, diagnosed differently than one from penaeids, can be treated with a dip or long-term dose of 100 ppm Terramycin (Figs. 4-6). Treated brine shrimp slough the bacterium as a single entire mat (Solangi et al. 1979). This infestation typically results from high organic levels in the water rather than from crowding.

When antibiotics are used extensively for a bacterial disease or for any purpose, penaeids or other crustaceans may increase their susceptibility to other conditions. Extensive mortalities of larval *Penaeus vannamei* and *P. stylirostris* from an unidentified ameoba appear to be a good example of what can happen when antibiotics are overused (Laramore and Barkate 1979).

FUNGI

Several species of fungi infect penaeids and other crustaceans, and some of them are seriously pathogenic to their hosts. Some lodge in the gill lamellae and cause "gill disease," a complex of several diseases caused by numerous organisms and conditions in addition to fungi. Gills can be destroyed or the host can suffocate from mechanical blockage (Lightner 1975). One of two serious causative agents of fungal disease is *Lagenidium* sp. In *P. aztecus* and *P. setiferus*, it causes mortality, primarily in protozoeal stages. Whereas malachite green oxalate and Treflan can be used to treat infections, separating healthy nauplii by using a bright light source seems to be more practical (Lightner footnote 2). *Fusarium solani* can be severely pathogenic to certain shrimps. Since various penaeids exhibit different degrees of susceptibility to this imperfect fungus, selection of shrimp-species for culture can be critical to economic success. Resistance by *P. californiensis* to infection is minimal compared with that by *P. aztecus* and *P. setiferus*. The two resistant shrimps quickly destroy low numbers of fungal spores in their gills, whereas the fungus kills most infected individuals of *P. californiensis* (see Solangi and Lightner 1976). Macroconidia actively enter abrasions in shrimp maintained in cement tanks. In order to prevent those lesions and subsequent infection, sand can be introduced into such tanks in sufficient quantity to allow shrimp to bury themselves.

CILIATES

Ciliates circulating in the hemocoel of various crustaceans (Couch 1978; Overstreet and Whatley 1975) have been reported, but they probably reproduce most extensively in already-stressed hosts, rather than being the cause of the original stress. An unidentified apostome (Figs. 7, 8) is another cause of "gill diseasc" (Overstreet 1978). It probably could cause problems in culture conditions, but appears to be benign in shrimp from their natural environment. Also, the peritrich *Zoothamnium* sp. on the gills of penaeids (Fig. 9) does not harm its host in the wild (Foster et al. 1978), but in crowded culture conditions it can heavily infest the gills and compete with the host for oxygen, especially when the dissolved oxygen concentration of the system drops to a low level (Overstreet 1973). This association is in contrast to *Epistylis* sp. on scaled fishes in southeastern U.S. estuaries and freshwater. That peritrich appears to erode the epithelium from the scale, sometimes even resulting in exposed flesh and bone, rather than to attach to a layer secreted by the ciliate (Lom 1973). *Aeromonas hydrophila*, a bacterium capable of liquifying host tissue without the ciliate present, may secondarily infect *Epistylis* sp.-infested fishes and cause serious disease and mortalities (Overstreet and Howse 1977). *Zoothamnium* sp. on shrimps can be controlled using up to 250 ppm Formalin for a short dip or 25 ppm for an indefinite period in a pond (Johnson 1974).

MICROSPORIDANS

Several species of microsporidans, each infecting different sites, make infected penaeid hosts unmarketable (Figs. 10, 11). They constitute serious threats to shrimp culture, especially in ponds or enclosed natural bodies of water where the cycle can more easily be completed. Preliminary studies in my laboratory have shown that different chemicals can be used to prevent infections in the related *Ameson michaelis* in the blue crab (Overstreet and Whatley 1975; Overstreet 1975).

DIGENEANS

Few metacercariae (opecoelids and microphallids) infect penaeids and these do not seriously harm their hosts unless infected by unusually large numbers. Heavy infections seldom occur except in experimental conditions (Fig. 12). The potential for

human infections of some microphallids does exist (Overstreet in press; Heard and Overstreet unpubl. data).

CESTODES

Several species of cestodes infect penaeids. These include tetrarhynchideans, tetraphyllideans, and at least one cyclophyllidean. Metacestode stages of tetrarhynchideans in the hepatopancreas attract the most attention because they often can be seen without a microscope through the host's carapace and consequently cause infected shrimp to be labeled "wormy" and unfit to eat. Penaeids infected with any of the several described tetrarhynchideans can be eaten raw without any worry of human infection with those cestodes. Other groups of parasites and disease agents in shrimps, of course, can infect man when products are eaten raw.

The cestode most often reported in shrimps is *Prochristianella hispida* (Figs. 13, 14). No life cycle of this or any other tetrarhynchidean has been demonstrated completely. Tom Mattis, in my laboratory, has nearly completed the cycle of *P. hispida*. Rather than having a single crustacean intermediate host as an addition to the dasyatid ray definitive host assumed in the literature, an intermediate copepod host also appears necessary to infect the penaeids and other shrimps. Because of the absence of elasmobranch hosts from or near most pond facilities, tetrarhynchideans and tetraphyllideans pose little threat to aquaculture. In their natural habitats, shrimps seldom are infected by cestodes or any other helminths in high enough densities to have a detrimental effect on stocks.

NEMATODES

Although nematode larvae (Fig. 15) pose little threat to the health of shrimps, at least one species will invade the gastrointestinal tract of a variety of mammals (Fig. 16). This ascaridoid, *Hysterothylacium* type MB, penetrates the stomach and upper duodenum of the rhesus monkey within a few hours after being administered (Overstreet and Meyer 1981). It causes mucosal hemorrhage and attracts local tissue eosinophils. In Mississippi, three distinct forms of *Hysterothylacium* spp. infect penaeids (Deardorff and Overstreet 1981), but only one has been demonstrated to invade mammalian tissue (with tests using mice—Norris and Overstreet 1976). The larval camallanid *Spirocamallanus cricotus* and other non-ascaridoid nematodes also infect various penaeids, but are typically uncommon in and probably have little effect on those shrimps.

MISCELLANEOUS STRESS CONDITIONS

When maintained densely in holding facilities, as is done by bait suppliers, penaeids and other shrimps often exhibit stress conditions. Two common conditions have been referred to as "spontaneous necrosis" and "cramps." In the former, abdominal muscles of affected shrimp degenerate when the shrimp undergoes stress from low oxygen concentration or rapid environmental changes (Lakshmi et al. 1978). If oxygen can be supplied or conditions can be improved considerably before the terminal portion of the affected shrimp turns chalky white, the progressive condition can reverse itself, and the shrimp may survive. A "cramped" shrimp develops a completely or partially flexed abdomen, usually in water conditions of low salinity and low temperature. The flexure becomes so rigid that it cannot be straightened. Affected shrimp can swim with this flexure until the imbalance of their internal ions becomes severe enough that they die (Venkataramiah et al. 1977 and Venkataramiah[4]).

Cultured shrimps are also prone to excess dissolved nitrogen (Lightner et al. 1974) and oxygen (Supplee and Lightner 1976), especially in heated water. "Gas-bubble disease" should be taken into account when designing culture facilities.

Numerous other parasites, conditions, and toxic substances infect or affect penaeids both in the United States and elsewhere. Some do and others will probably on occasion have a strong influence on individuals or stocks both in culture and in their natural habitats. Some of these are discussed or reviewed in papers by Overstreet (1973, 1978), Lightner (1975), Johnson (1974, 1978), Overstreet and Van Devender (1978), and Couch (1978, 1979).

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The Helminths and Commensals of Crustaceans of the Black Sea

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ABSTRACT

Twenty species of organisms, epibiontic on crustaceans, of the Black Sea, are typical parasites. They are larvae of trematodes, cestodes, nematodes, and acanthocephalans. It is interesting that only one of nine of the larval trematodes completes its development in fishes. The other eight species complete their development in marine birds.

The ciliate fauna associated with marine littoral crustaceans in the Black Sea numbers 35 species. The species of *Zoothamnium*, *Heliochona*, and *Cothurnia* occurred in great numbers everywhere. The frequency of infection varied between 70 and 100%.

The pathogenicity of helminth and ciliate infections was not observed.

INTRODUCTION

Study of the parasite fauna of crustaceans of the Black Sea is relatively recent. The roles of certain common species of mollusks in the life cycles of trematodes [digeneids] of the Black Sea have been determined already (Dolgikh 1965), but further clarification of the role of invertebrates of this body of water as carriers of parasitic organisms is of certain practical and theoretical interest.

The present paper describes the infection of certain littoral crustacean species of the Black Sea coast. We examined about 35,000 individual crustaceans of the following species and subspecies: *Altlutha typica*, *Tisbe* sp., *Palaemon elegans*, *P. adspersus*, *Crangon crangon*, *Hippolyte longirostris*, *Diogenus pugilator*, *Clibanarius crythropus*, *Carcinus maenas*, *C. mediterraneus*, *Macropipus holsatus*, *Pilumnus hirtelus*, *Eriphia verricosa*, *Xantha poressa*, *Pachygrapsus marmoratus*, *Tanais carolini*, *Sphaeroma serratum*, *Nassa bidentata*, *Idothea baltica*, *I. baltica basteri*, *Synisoma capito*, *Nalophilosa fucarum*, *Gammarus subtypicus*, *G. aequicauda*, *G. insensibilis*, *G. olivii*, *G.* sp., *Gammarellus carinatus*, *Orchestia gammarella*, *O. bottae*, *O. mediterranea*, *O. montagui*, *Hyale pontica*, *Ploenexes gammaroides*, *Corphium bonelli*, *Caprella danilevskyi*, *C. acanthifera*, and *Zigia italica*.

The crustacean host material was collected at three localities: 1) In the Black Sea along the west coast of Crimean Karadag; 2) in the bays of Sevastopol (i.e., Kazatchaya, Streletskaya, Omega, Karantinnaya, Kamyshovaya, Martynova, and Konstantinovskaya Bays); and 3) in the Karkinitsky creek and the Egorlitsky estuary.

The crustaceans examined represent only a small portion of the species of invertebrates of the Black Sea and their populations. Undoubtedly, the ciliate associates of decapods reported by us are but a small fraction of those which actually occur. The pathogenicity of the helminth and ciliate infections was not observed. In spite of the infection mode of some ciliate species, they evidently are harmless commensals.

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PROTOZOANS

CLASS CILIOPHORA

Heliochona pontica Jankovski, 1970—Belongs to an order, all species of which are ectocommensals of Crustacea, presently found mostly on the free edges of the gills of *Gammarus olivii* and *G. insensibilis*. It occurs by the thousands on the gills of the hosts in summer in three regions of Karadag and in several Sevastopol bays (i.e., Omega, Karantinnaya, and Martynova). Jankovski (1970) described this species from *Gammarus* sp. along the coast of Yalta.

Epistylus amphitae Naidenova, 1980—Numerous colonies consisting of four to six zooids at the base of the pleopods on the abdomens of *Amphitae vallenti*. This ciliate was found in Martynova Bay (Sevastopol) in summer.

Epistylus sevastopoli Naidenova, 1980—On the mouth parts of the crab *Pachygrapsus marmoratus*. A few colonies, rarely of more than six individuals, were found in Omega Bay in summer.

Myoschiston duplicatum Precht, 1935—Numerous low colonies on the abdomen of the isopod *Idothea baltica* were found in Omega and Pesotchanaya Bays along the coast of Karadag. This species was described by Precht (1935) who found it on isopods and crabs from Kieler Bucht.

Intrastylum sp.—Single specimens were found on the abdomen of *Gammarus insensibilis*, which live along the coast near Sevastopol (Omega Bay, Kazatchaya Bay).

Carschesium gammari Precht, 1935—Heavily infecting the antennae and mouth parts of *Gammarus insensibilis* were found in Omega Bay. The maximum infection occurs at the end of summer and in autumn. This species was described by Precht (1935), who found it on gammarids from the Baltic Sea.

Vorticella micra Naidenova, 1980—Single zooids were observed on the body cuticle of the crab *Carcinus maenas* of the Sevastopol coast in summer.

Vorticella idothea Naidenova, 1980—Rarely occurred on the abdomen of *Idothea baltica* in the warm time of year in the Sevastopol and Karadag regions.

Vorticella companula Ehrenberg, 1831—Single specimens occurring on the tests of crabs (*Carcinus mediterraneus*) and isopods (*Idothea baltica*) were found in spring near Sevastopol. This species was previously known from the Black Sea as a free-living form.

Vorticella minima Naidenova, 1980—This ciliate was found on the posterior segments of the abdomen of the isopod *Sphaeroma serratum*. Of rare occurrence near Sevastopol in spring.

Vorticella striata Dujardin Kent, 1841 [(Dujardin 1841) Kent?] —This ciliate lives in small numbers on the body surfaces of the crab *Macropipus holsatus* and two species of isopods, *Idothea baltica* and *Nassa bidentata*. It is found in all localities of Sevastopol bays and along the coast of Karadag. This species has been described as free-living but was not found in the Black Sea earlier. Precht (1935) recorded it as an ectocommensal of many invertebrates of the Baltic Sea.

Vorticella sphaeroma Naidenova, 1980—This species occurred singly on the body surface of *Sphaeroma serratum* in Sevastopol bays in the spring and autumn.

Vorticella nebulifera O. F. Müller, 1773—On the body surface of *Carcinus mediterraneus* and *Idothea baltica* near Sevastopol. This species was recorded as habitually free-living in the Black Sea, by Mereschkovski (1880) and Dagaeva (1928).

Vorticella convallaria (Linnaeus, 1767)—Occurred singly on the carapace of the crab *Carcinus mediterraneus* along the coast of Sevastopol in summer. This species was found free-living by Mereschkovski (1880) along the Crimean coast and by Buschinski (1897) in Odessa creeks.

Vorticella claparedi Andrusova, 1886—Found in low numbers on the carapace and telson of the crab *Carcinus mediterraneus* along the coast of Sevastopol. This species was also described as free-living in the Black Sea by Andrussova (1886).

Vorticella lima Kahl, 1933—Found on the legs of *Sphaeroma serratum* and *N. bidentatum* from localities on the Karadag and Sevastopol coast.

Vorticella microstoma Ehrenberg, 1830—Occurred rarely on the legs of the crab *Carcinus mediterraneus* and the isopod *Idothea baltica* in Omega Bay (Sevastopol) in summer. Gaevskaya (1924) and Dagaeva (1928) reported this species as free-living in the Black Sea.

Vorticella patellina O. F. Müller, 1776—This species was observed on the body surfaces and legs of the crabs *Carcinus mediterraneus* and *Macropipus holsatus* from localities in Omega Bay. It was reported by Precht (1935) as a commensal of invertebrates in the Black Sea.

Zoothamnium sevastopoli Naidenova, 1980—A great number of colonies, of as many as 200 individuals, were counted on the single side-plates and anterior peraeopods of *Gammarus olivii* and *G. insensibilis* from Sevastopol bays and Karadag all year round. In spring and summer their number reaches some thousands on gammarids.

Zoothamnium ponticum Perejaslawzewa, 1886—Small colonies, usually consisting of only five to eight zooids, occurred on the dorsal side of *Gammarus insensibilis* from Sevastopol in autumn. This ciliate has been described previously as free-living from the Black Sea.

Zoothamnium alternans Clap. et Lachm., 1858—Tall, slender colonies, consisting of up to 17 individuals, were attached to the abdomens of the isopod *Sphaeroma serratum* and on the legs of the crab *Carcinus mediterraneus*. This ciliate was often found on crustaceans from Karadag waters, rarely in Sevastopol Bay.

Zoothamnium duplicatum Kahl, 1933—This species was mostly found on the pleopods of *Gammarus* sp. examined in Karadag region. About 20 colonies consisting of two to eight individuals were observed. This species is recorded as an ectocommensal on gammarids from Scandianavian waters by Fenchel (1966) and Precht (1935).

Zoothamnium laomedeae Precht, 1935—Small colonies, usually consisting of only two individuals, were observed on the legs of *Gammarus insensibilis* from Sevastopol bays. This species was recorded by Perejaslawzewa (1886) as free-living in the Black Sea.

Zoothamnium nanum Kahl, 1933—Numerous colonies occurred on the body surface of *Idothea baltica*. This ciliate is regularly found on isopods from Sevastopol waters in summer and autumn. The species is known from the Black Sea as a free-living form.

Zoothamnium sphaeroma Naidenova, 1980.—Numerous colonies consisting of 2 to 20 zooids were always found on the gills of *Sphaeroma serratum* from two Sevastopol bays (Omega and Kruglaya) and along the coast of Karadag. This species is encountered all year round.

Zoothamnium perejaslawzeva (Perejaslawzewa, 1886)—High, slender colonies consisting of about 200 zooids were often observed on the dorsal surface of *Sphaeroma serratum* from Omega Bay in early spring. This ciliate was described from the Black Sea as free-living.

Cothurnia achtiari Naidenova, 1980—Always found on legs of *Sphaeroma serratum* and *N. bidentata*. Up to 20 individuals were counted on a single isopod in Sevastopol waters. They are especially numerous in spring.

Cothurnia sevastopoli Naidenova, 1980—The most numerous species of this genus, it occurs on the abdomen and leg bases of *Gammarus olivii* all year round. Maximum infection was recorded at the end of summer and in early autumn in several Sevastopol bays (i.e., Martynova, Kazatchaya, and Omega).

Cothurnia gammari Precht, 1935—Found on the abdomen and pleopods of *Gammarus insensibilis* from Omega Bay. This is a characteristic ciliate of gammarids from Scandinavian waters (Precht 1935; Fenchel 1966).

Delamurea loricata Naidenova, 1978—Each colony may consist of up to 32 zooids. Numerous colonies were found in the

pseudolorica on the abdomen of *Sphaeroma serratum*. It occurred at all localities in three Sevastopol bays (i.e., Martynova, Karantinnaya, and Pesotchnaya). In winter they are encountered rarely as single findings. In spring and summer infection reaches some hundreds.

Delamurea maeatica Naidenova, 1978—Occurred in colonies usually consisting of only two to four zooids and never of more than six. The pseudolorica are attacked at the junction between the rami and the peduncle of the pleopods of *Sphaeroma serratum*. They are found in all localities in the Sevastopol bays all year round.

Tanriella lomi Naidenova, 1980—Low colonies surrounded with a "collar" occurred rarely on the gill bases of *Sphaeroma serratum*. They are encountered in summer along the coast of Karadag and Balaklava. The colonies are small, consisting of up to 12 zooids.

Gymnodinoides sp.—The phoronts always occurred as small groups of 5 to 15 individuals at the junction of each pleopod and on the abdomen where they could be seen rotating in their cysts. The maximum number of cysts was noted in spring. The phoronts were found in localities on all species of gammarids examined in several Sevastopol bays (i.e., Martynova, Omega, Streletskaya, and Kasatchaya). Fenchel (1966) noted the settlement of phoronts of the species *Gymnodionoides irkystans* on gammarids of the Baltic Sea.

Aceneta tuberosa Ehrenberg, 1833—This suctorian was numerous in autumn on the crabs *C. mediterraneus*, *Macropipus holsatus*, and *Sphaeroma serratum*. It could be found in various places on the host's body. It was found in Sevastopol bays, along the coast of Karadag. It has been recorded as free-living in the Baltic Sea.

Aceneta foetida Eichwald, 1847—This species is numerous in autumn on the legs of *Gammarus olivii* from all localities along the coast of Sevastopol.

HELMINTHS

CLASS DIGENEA

Family Opecoelidae Ozaki, 1926.

Helicometra fasciata Rudolphi, 1819—Metacercariae were found in muscles of the shrimps *Palaemon elegans* and *P. adspersus*. Intensity of infection was up to 22/host. The first species was the most heavily infected (30%). Metacercariae were found in several Sevastopol bays (i.e., Omega, Kazatchaya, and Streletskaya), along the Balaklava coast. The final hosts of these trematodes are many species of littoral fishes (Gobiidae, Labridae, etc.) (Naidenova and Dolgikh 1969).

Family Microphallidae Travassos, 1920.

Microphallus papillorobustus (Rankin, 1940)—Metacercaria usually were localized in the body cavity of *Gammarus subtypicus* and *G. aequicauda*. The sites of localization were Karkinitsky Creek, the Egorlitsky estuary, and the Sevastopol coast. Mature forms infect the marine birds *Larus melanocephalus* and *Larus genei*, Limicolae (Smosorzhevskaya 1979). Intensity of infection was up to 37. The maximum infection was registered in Karkinitsky Creek (87%) in summer.

Microphallus hoffmanni (Rebekq, 1964)—Localized in the body cavities of *Gammarus insensibilis*, *G. subtypicus*, and *G. aequicauda* inhabiting the Egorlitsky esturary and the Sevastopol bays. Infection intensity was up to 174. Infection of up to 57% of the hosts was characteristic for these regions in late summer and in autumn. Mature specimens were found in the bird *Numenius arquata* (Iskova 1967).

Microphallus claviformis (Brandes, 1888)—Occurred in the body cavity of *Idothea baltica basteri* from the Egorlitsky estuary. Infection intensiveness was from one to four. The infection was not high. The final hosts are the birds *Tringa hypolencos*, *T. totanus*, *Charadrius alexandrinus*, *Recurvirostra ovosetta*, *Squatorola squatorola*, *Arenaria interpres*, *Vanellus vanellus*, and *Anas acuta* (Belopolskaya 1966; Iskova 1968; Smogorzhevskaya 1976).

Levinseniella bucephalae (Yamaguti, 1936)—Displayed on *Gammarus aequicauda*, *G. subtypicus*, and *G. insensibilis* in two Sevastopol bays (Kazatchaya and Omega) and in the waters of the Egorlitsky estuary. Infection was low (up to 6%), and intensity was up to 12 per individual host. Mature trematodes inhabit the intestine of the bird *Tadorna tadorna* (Iskova 1968).

Levinseniella sp.—Found singly in the body cavity of *Gammarus insensibilis* in Omega Bay.

Maritrema subdolum Jägerskiöld, 1909—Found in the body cavity of *Gammarus insensibilis*, *G. subtypicus*, and *G. aequicauda* with an intensity of up to 35. They were found also on *Idothea baltica basteri* with an intensity up to 300 specimens in the Sevastopol bays, Karkinitsky Creek, and the Egorlitsky estuary. In Karkinitsky Creek, infection is 100% of the last species. *Gammarus* infection is only 50 to 71%. Mature trematodes are common for the birds of the groups Limicolae and Lari and rare for Steganopodes and Anseres (Leonov 1958; Smogorzhevskaya 1976; Garkavi 1965).

Gynaecotyla longintestinata (Leonov, 1958)—Metacercariae were found in kidneys of the crabs *Carcinus mediterraneus* and *Macropipus holsatus*, in the Sevastopol bays and along the coast of Karadag. Intensity of infection was up to 180 specimens and infection was 24.2%. The final hosts are herring gulls, *Larus argentatus*.

Microphallidae gen. sp.—Seldom found on gills of the shrimps *Palaemon elegans* and *P. adspersus* in Sevastopol bays and along the coast of Evpatoria. Intensity of infection was not high (1-17%).

CLASS CESTODA

Family Tentaculariidae Poche, 1926.

Nybelinia sp.—Found as single larvae in the body cavity of *Gammarus insensibilis* in Omega Bay. In the Black Sea, *Nybelinia lingualis* larvae are recorded from the intestines of pelamida, *Sarda sarda* (Reshetnikova 1955).

Family Lecistozhynchidae Guiart, 1927.

Christianella minuta—Larvae were noted in the liver of *Pilumnus hirtelus*. Intensity was up to five in the Egorlitsky estuary. Infection reached 23.3%. Mature cestodes parasitize the fishes *Raja clavata*, *Dasyatis pastinaca*, and *Squalus acanthias* (Karnoshin and Solonchenko 1978).

Family Phyllobothriidae Broun, 1900.

Scolex pleuronectis Muller, 1788—Single individuals were found in the intestines of *Carcinus mediterraneus* and *Clibanarius erythropus* in Pesotchanaya Bay (Sevastopol region). Larvae of more than 20 species are widely dispersed in many kinds of fishes of the Black Sea.

PHYLUM ACANTHOCEPHALA

Family Echinorhynchidae (Cobbold, 1879) Hamman, 1892.

Metechinorchynchus truttae (Schrank, 1788)—Found singly in muscles of *Gammarus subtypicus* in the waters of the Karkinitsky Creek region. Mature Acanthocephala are registered for the fishes *Salmo truttae labrax* and *S. truttae labrax* v. *locustris* in the waters of the Caucasus region (Kurashvili 1960, 1967).

Family Telosentidae, Petrotchenko, 1956.

Telosentis exiguus Linstow, 1901—Single larvae were found in the body cavity of *Gammarus insensibilis* and *G. aequicauda* in the waters of three Sevastopol bays (Kazatchaya, Streletskaya, and Omega). Mature forms are common parasites of many Black Sea fishes.

Family Rhadinorhynchidae Travassos, 1923.

Golvanacanthus problematicus Mordinova and Parukhin, 1978—Found individually on *Gammarus olivii* in Omega Bay (Sevastopol). Adult forms are known only from the Mediterranean Sea.

CLASS NEMATODA Rudolphi, 1808

Family Proleptidae E. Skrjabina, 1968.

Proleptus sp.—Single larvae were found in the body cavity of the crab *Carcinus mediterraneus* in Streletskaya Bay. Only one species of the genus, *Proleptus robustus*, is known in the Black Sea. It parasitizes the intestines and stomach of *Raja clavata* (Osmanov 1943; Naidenova and Nikolaeva 1964).

Family Rhabdochonidae Skrjabin, 1946.

Ascarophis sp.—Displayed in the muscles and gills of the crabs *Pachygrapsus marmoratus* and *Xantha poressa* and the shrimps *Palaemon elegans*, *Gammarus olivii*, and *Orchestia bottae*, in two Sevastopol bays (Omega and Martynova). Infection is low. Intensity is up to 4%.

Family Anisakidae Skrjabin and Karokhin, 1945.

Contracaecum filiforme (Stossich, 1904)—Single specimens were found on [in] the liver and stomach of the crab *Carcinus mediterraneus* in Kazatchaya Bay. Mature nematodes inhabit the fishes *Uranoscopus scaber* and *Contracaecum aduncum* (Rudolfi 1802). Infection was 7.5%. Intensity was up to 15 specimens. These nematode larvae infect many Black Sea fishes. Mature forms parasitize predatory fishes, such as *Scomber scomber*, *Umbrina cirrosa*, *Belone belone euxini*, and *Odontogadus merlangus euxinus*, etc. (Pogoreltseva 1952; Kovalaeva 1970; Naidenova 1974).

Family Spiruridae Oerly, 1885.

Spiruridae gen. sp. 1—Single larvae were found in the muscle of *Pachygrapsus marmoratus* in Martynova Bay.

SUMMARY

The present ciliate fauna associated with the marine littoral crustaceans in the Black Sea numbers 35 species. The *Vorticella* species habitually are found on the body surfaces of crabs, isopods, and gammarids. Almost 100% of all littoral crustaceans were infected. They are encountered rarely and in low numbers, compared with free-living forms. The ciliates of the Black Sea have been studied inadequately, therefore it is difficult to determine whether they are commensals or accidentally found [accidentally occur on these host organisms]. The species of *Zoothamnium*, *Heliochona*, and *Cothurnia* occur in great numbers everywhere. Infection frequency varied between 70 and 100%.

Investigation of the rate of reproduction of ciliate ectocommensals on marine crustacean species disclosed their considerable role in the productivity of the benthic populations.

Thus, 20 species of organisms, epibionts of crustaceans of the Black Sea, are typical parasites. They are intermediate stages of trematodes [digeneids], cestodes, nematodes, and acanthocephalans. It is interesting that only one of nine species of larvae of trematodes [digeneids] completes its development in fishes. *Helicometra fasciata* is a mass parasite of the intestines of littoral fishes. Shrimps make up a great part of their food. The majority of the invertebrates examined are inaccessible for [not included in] fishes' diet. This explains why they [fishes] are absent among the second intermediate hosts of trematodes. It is interesting as well that cestode and nematode larvae, connected with large predators such as sharks and rays, occur in crabs. Larvae of nematodes and trematodes [digeneids] are found in crabs which are included in the food spectrum of predatory fishes—sharks, rays, and scombrids. They are the final hosts of helminths. The other eight species of trematode larvae complete their development in marine birds. All of the metacercariae we found are connected with the site inhabited by the proper [appropriate] hosts. The land banks of Karkinitsky and Egorlitsky Creeks shelter great colonies of birds. Their food spectrum includes littoral invertebrates such as *Gammarus*, *Idothea*, and crabs. They are intermediate hosts of trematodes. It is interesting that metacercaria trematodes of birds—ducks of Omega Bay—are found in *Gammarus*. The findings of nematodes, cestodes, and acanthocephalans are single [?]. They complete their life cycles in fishes. All acanthocephala larvae are found in small invertebrates. Their life cycle is connected with fishes inhabiting the littoral-thicket biocenosis [swamps or wetlands].

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Achievements of Soviet Scientists in Investigations of the Helminthofauna of Marine Mammals of the World Ocean [1,2]

S. L. DELAMURE and A. S. SKRIABIN[3]

ABSTRACT

During the last 40 yr (1940 to 1980), Soviet helminthologists have examined about 9,680 specimens of marine mammals in the Northern and Southern Hemispheres, using uniform or standard methods in most cases. As a result, 20 new species of trematodes [digeneids], 19 cestodes, 9 acanthocephalans, and 23 nematodes have been described. Also several new supraspecific taxa have been established. Systematic revisions of Campulidae, Tetrabothriidae, Pseudaliidae, and Anisakidae have been undertaken.

The morphology, adaptation of helminths to their environments and to the host's mode of life, infection rates and characteristics, and the seasonal and age dynamics of the helminthofauna have been studied. Methods of distinguishing host populations using quantitative and qualitative differences as well as the geographic variability of the helminthofauna have been developed. Consequently local stocks of mammals have been revealed, as has the pathogenicity of several helminth species.

All of these data have been summarized from ecological, zoogeographical, and phylogenetic points of view. Results of these studies are now employed by zoologists interested in sea mammals.

In 1780 Fabricius published a scientific description of the cestode *Pyramicocephalus phocarum* (Fabricius, 1780), the first of the helminth species to become known to science as a parasite of marine mammals. Some time later Karl Rudolphi (Rudolphi 1802 to 1819) described another eight species (trematodes [digeneids], cestodes, and acanthocephalans) parasitizing these animals. Without becoming too immersed in the history of the development of knowledge of the parasites of marine mammals (for details see Delamure 1955), we wish to indicate that over the last 200 yr (1780-1980) some 276 species of helminths infecting marine mammals of the World Ocean have been discovered by Soviet and foreign scientists.

Today the parasites of these animals are of interest, not only to parasitologists but also to mammalogists studying marine mammals. They are attracted by the possibilities of using helminthological data for the purposes of studying the ecology, phylogeny, dynamical statistics [population dynamics?], and the population structure of the [various] species of marine mammals, including those of commercial importance.

Helminths of marine mammals are not without significance to medical and veterinary specialists, especially since it is known that there are pathogenic species common to pinnipeds, cetaceans, wild and domestic terrestrial mammals, and also to man: *Opistorchis felineus* (see Kurochkin 1960); *Diphyllobothrium cordatum* (see Yamaguti 1959); *D. pacificus* (see Atias and Catton 1976); *Pyramicocephalus phocarum* (see Rausch et al. 1967); *Taenia solium* larvae (see Graff et al. 1980); *Trichinella spiralis* (see Rausch et al. 1956; Fay 1960; Smirnov 1963; Kozlov 1966, 1971; Treshev and Serdukov 1968; Arvy 1970); larval Anisakidae (Kurochkin and Mamaev 1972; Shiraki 1974; and others).

The interest which has developed in studying helminths of marine mammals will be illustrated by examining the dynamics of recent publications by 10-yr periods.

Before 1940 Soviet scientists had published eight works in this one area. Between 1941 and 1950 they published 15, from 1951 to 1960—31, from 1961 to 1970—91, and from 1971 to 1980—143 articles.

According to the summary of Scheffer and Rice (1963), the World Ocean is inhabited by 31 species of pinnipeds and 80 species of cetaceans. Not all of them have been studied in helminthological respects. Better known than others are the helminthofaunas of the walrus and long-eared seals of the Northern Hemisphere, the true seals and major commercial whales of temperate and cold waters of the Northern and Southern Hemispheres, and, likewise, certain species of small whales. This is due, in no small measure, to Soviet scientists who for the first time investigated the helminthofauna of the gray whale (Treshev 1966a); Bryde's whale (Skriabin 1970a); harbor seals inhabiting the Bering Sea (Yurakhno 1970); island seals (Nikolsky and Kazikanov 1970); small seals of the Baltic Sea and Lake Ladoga (Barysheva and Bauer 1957; Delamure et al. 1980); Caspian seals (Schupakov 1936; Kurochkin 1958; and others); and the Baikal seal (Sudarikov and Ryzhikov 1951; Delamure et al. 1979a; and others).

In this connection it should be indicated that in the last 40 yr Soviet helminthologists have examined 9,680 marine mammals from various zones of the World Ocean (pinnipeds—6,222 and cetaceans—3,458). The large majority of those examinations (8,432) were carried out using the same accepted methodology (Delamure and Skriabin 1965b), by colleagues of the chairman of Zoology of the Crimean Pedogogical Institute (since 1972, the Simferopol State University), by participants in the 33 expeditions to the Black, Azov, Caspian, Baltic, Greenland, Barents, White, Eastern Siberian, Chukchi, Bering, and Okhotsk Seas;

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[2]The text and Literature Cited sections of this paper were translated from the Russian by W. J. Hargis, Jr., with assistance of fellow students in the 1982 Russian scientific reading course of the School of Marine Science of the College of William and Mary. Despite the assistance of colleagues, the translator-editor must assume full responsibility for its accuracy and faithfulness of style. The abstract portion of the paper was translated by O. N. Bauer of the Zoological Institute of the Academy of Sciences of the U.S.S.R.

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Lakes Ladoga and Baikal; and expanses of the Southern Hemisphere—including the waters of the Antarctic. Regarding our waters, we have not as yet been able to investigate the marine mammals of the Karskogo Sea and the Sea of Laptevykh.

Turning now to the most common results of the efforts of Soviet scientists in faunal areas, it is interesting to compare them with analogous investigations performed abroad. Calculation has shown that until 1900 only 16 species of trematodes, parasitic in pinnipeds and cetaceans, were known, but now there are 72. During the last 40 yr 27 species have been described (principally of the families Campulidae, Notocotylidae, and Microphallidae). Of that number, 20 or 74% have been by Russian scientists (Skriabin 1944, 1947; Krotov and Delamure 1952; Gubanov *V. Kh.*: [*in*:] Delamure 1955;[4] Delamure and Kleinenberg 1958; Kurochkin 1958, 1962; Skriabin 1959, 1969a, 1970a; Petrov 1963; Treshev 1966a, 1968; Yurakhno 1967, 1968, 1969; Treshev et al. 1969; Kurochkin and Nikolsky 1972. New taxa have been established—the genera *Oschmarinella* Skriabin 1947; *Leucasiella* Krotov and Delamure 1952; *Cetitrema* Skirabin 1969a; and the family Campuloidea (A. Skriabin 1976).

Significant progress has been made in the studies of the cestodes parasitizing marine mammals. Known at present are 71 species of cestodes (versus only 20 in 1900). These discoveries include interesting tetrabothriid species (of the genera *Tetrabothrius*, *Priapocephalus*, and *Trigonocotyle*) and diphyllobothriids (of the genera *Diphyllobothrium*, *Diplogonoporus*, *Tetragonoporus*, *Hexagonoporus*, and *Polygonoporus*). Of the 32 cestode species described in the last 40 yr, some 19 (or 59%) have been by Soviet scientists (Gubanov in Delamure 1955; Delamure 1955, 1971; Belopolskaya 1960; Skriabin 1961, 1967; Delamure et al. 1964; Delamure and Skriabin 1966; Delamure and Parukhin 1968; Muraeva and Treshev 1970; Yurakhno 1973). New genera have been established (*Tetragonoporus* Skriabin, 1961; *Hexagonoporus* Gubanov in Delamure 1955; *Polygonoporus* Gubanov in Delamure 1955; and *Polygonoporus* A. Skriabin 1968); and a subfamily, Polygonoporinae Delamure and Skriabin 1968. Occupying a special place is the discovery by A. Skriabin of a 30 m long diphyllobothriid, *Polygonoporus giganticus* A. Skriabin, 1967, parasitizing the cachalot, with strobilae about 5 cm wide, having some members [strobilae] with 14 gonads in the sexual complex.[5] Diplo- and polygonadal diphyllobthriids have been the subject of special investigations which attempt to clarify their systematics and phylogeny (Delamure and Skriabin 1966, 1968). There have been studies of larval forms or stages of cestodes invading cetaceans (Delamure 1955; Skriabin 1965, 1970a, 1971).

Research has added significant information about acanthocephalans. At present, 35 species parasitizing pinnipeds and cetaceans are known (versus 8 in 1900). Since 1940, 19 species have been described (of the genera *Bolbosoma* and *Corynosoma*). Of these, nine have been described by Soviet scientists (Krotov and Delamure 1952; Gubanov in Delamure 1955; Skriabin 1959; Treshev 1966a, 1970; Nikolsky 1974a).

By 1900, 23 species of nematodes were known from marine mammals; at present there are 98. In the last 40 yr, 46 species have been discovered (of the families Pseudaliidae, Folaroididae, Crassicaudidae, Anisakidae, and Capillariidae), of which 23 (50%) were described by Russian scientists (Skriabin 1933, 1942; Delamure in Skriabin 1942; Delamure 1946, 1951a; Gubanov 1951; Mozgovoy 1951; Gubanov in Delamure 1955; Kurochkin and Zablotski 1958; Skriabin 1959, 1966, 1969a; Delamure and Alekseev 1966; Delamure and Kleinenberg 1968; Zablotski 1971; Yurakhno and Skriabin 1971; Nikolski 1974a). The new genera, *Otophocaenurus* Skriabin, 1942; *Skrjbinalius* Delamure in Skriabin, 1942, *Placentonema* Gubanov, 1951; and *Delamurella* Gubanov in Delamure 1955, were established. The discovery of the 9 m long nematode (*Placenotrema gigantissima* Gubanov, 1951), which parasitizes the placenta of cachalots by H. Gubanov deserves special attention.

At present 276 species of helminths parasitizing pinnipeds and cetaceans of the World Ocean are known. In addition to the Soviet scientists contributing significantly to knowledge of the helminth fauna during the last decade, one must acknowledge investigators from other countries, especially Baylis, Baer, Davey, Dailey, Dollfus, Dougherty, Margolis, Markowski, Rausch, Stunkard, Shultz, and Yamaguti.

The study of helminths of marine mammals has not been limited to discovery of new species, to redescription of old ones, to creation and revision of higher taxa, to studies of morphology and systematics, to development of better characteristics to clarify synonymies and permit more exact definitions, or to the discovery of principal hosts. In recent times there has been a change not only toward consideration of the morphological variables of the helminths of marine animals but also toward comparison of the factors of development, host-parasite relationships, zoogeography, and variables of routes and intensity of infection. Manifestations of the variability of different, separate indicators and also the causes of that variability have important meanings for the systematics of helminths and for the study of the population structure of their hosts—pinnipeds and cetaceans.

Study of the accumulated materials permitted revision of the taxonomic characteristics of marine mammals according to the taxa of helminths such as ampulids, tetrabothriids, pseudaliids, and anasakids (Skriabin 1942; A. Skriabin 1970a; Kontrimavichus et al. 1976; Temirova and Skriabin 1978; and others).

Helminths are not second in any respect to other animals in the number of their adaptations toward their environments and the life histories of their different hosts; e.g., those of the pseudaliid infecting the respiratory organs of dolphins (Delamure 1951a, 1955), as well as those of the crassicaudid nematode which infects the genito-urinary systems of whales (Skriabin 1969a). The origin of their adaptations is closely connected with those changes which the whales underwent in the course of their evolution.

The adaptations of gigantic cestodes and nematodes, which assure survival of the species over the wide expanses of the ocean, are very interesting (Delamure and Skriabin 1965a, 1968). Adaptation of the parasite to the anatomical and physiological peculiarities of the principal hosts together with the damage it causes have been studied by Skriabin (1960) using *Placentonema gigantissima* as a model or example. The importance of such investigations to the understanding of the host-parasite system is evident. Attempts have been made to study the life cycles of helminths of marine mammals. The studies of A. V. Uspenskaya (1960), who deciphered the life cycle of the nematode *Terranova decipiens*, and T. I. Popova, A. A. Mosgovoy, and M. A. Dimitrienko (1964), who devoted attention to the same question, are relevant. A. A. Mozgovoy, T. I. Popova, and V. I. Shakhmatova (1963) studied the life cycle of *Parafilaroides gymnurus* and B. E. Sudarikov and K. M. Rhyzhikov (1951) attempted to comprehend the cycle of *Contracaecum osculatum baicalensis* under the conditions found in Lake Baikal. These investigations supplement the findings of H. M. Pronin et al. (1980). Incidentally, comparison of

[4] *V. Kh.* seems to translate best as "in the work" or "in the work of," which can be reduced to "in" as it has been throughout this translation.

[5] This phrase concerning the sexual complex was particularly difficult to translate. It is hoped that it is correct, but may not be.

the helminth fauna of the Baikal seal, *Pusa siberica*, with the helminth fauna of other seals disclose their similarity to the species of the genus *Phoca* inhabiting the Asiatic sector of the northern Pacific and the Arctic and in no way supports their similarity to the helminth fauna of the Caspian seal, *Pusa caspica* (Mozgovoy and Ryzhikov 1950; Delamure et al. 1978). Comparative studies of the helminth fauna of the Caspian seals over an extensive period of time confirm the thesis of V. A. Dogiel (1947) regarding the relict parasite fauna having adapted its patterns to those of the host (Delamure et al. 1964, and others).

Massive examination of pinnipeds conducted over the last few years allows us to approach, for the first time, study of the intensity and extensiveness [prevalence] of invasion or infestation, seasonality, and growth dynamics of the helminthofauna of commercial marine animals inhabiting the waters of the Soviet Union and adjacent waters. Walruses, polar bears, sea lions, greenland seals, ringed seals, common seals (harbor seals), island seals, ribbon seals, bearded seals, and hooded seals were investigated from these points of view (Delamure and Treshev 1966; Treshev and Popov 1970, 1975; Delamure and Popov 1975; Kovalenko 1975; Popov 1975; Delamure et al. 1968, 1976).

It was established that the harbor seals inhabiting the Bering Sea begin to be infected by helminths at about 1 to 1.5 m in size when they cease feeding from their mothers and proceed to live and acquire nourishment independently. By the age of 2 mo the seal is usually attacked by two to four species of helminths. Later the infections increase very quickly and by the age of 4 [yr] the seals are struck [infected] by up to 12 species of helminths. In animals older than 12 yr of age a certain decline can be detected (9 to 10 species) [down to 9 to 10 species], which can possibly be explained by the changing ecology of the host. It is characteristic that in several species, infections become more intensive and also extensive [prevalent] as the seals grow but they are especially great or large in the young and also in the very old animals (Delamure and Alekseev 1962; Delamure et al. 1978; Treshev 1969; Yurakhno 1970b).

The generalized methodology for differentiating the populations of marine mammals, based upon the study of the qualitative and quantitative differences in their helminthofauna and also the geographical variability of the helminths (Delamure et al. 1979a; Popov and Marichev 1979) by comparison of the helminthofaunas and the characteristics of infestation of the different populations of marine mammals, demonstrated localized herds of walrus, Greenland seal, ringed seal, harbor seal, bearded seal, and the striped whale of the northern Pacific. It has also unearthed or disclosed the boundaries of the summer habitations [ranges, grounds, or habitats] of a certain population of whales of the Southern Hemisphere (Skriabin 1958, 1970a, 1972, 1975, 1978; Shustov 1965; Treshev 1970, 1978; Yurakhno 1970a; Kosygin and Popov 1972; Delamure and Popov 1978, 1980; Delamure et al. 1978, 1979a). These investigations confirm the opinions of mammalogists that existing stocks of pinnipeds and cetaceans must be protected. A comparison of the character [or nature] of infection with the findings (or data) of mammalogists on the mortality of seals permitted the assumption that helminths are one of the causes of their deaths.

Combining these data with histopathological investigations confirms the fact that pinnipeds whose hearts are stricken by the nematode *Dipetalonema spirocauda* perish during the first years [first year or early years] of life (Delamure et al. 1965; Delamure and Treshev 1966; Treshev et al. 1967; and others). Intensive infections of Baikal seal by the nematode *Contracaecum osculatum baiculensis* lead to the formation of large ulcers and fistulas in the walls of their stomachs and cause internal bleeding. Such a picture has been established from those animals which were killed during commercial harvesting and those which perished naturally and washed up on the shores of the lake by waves (Zhaltsanova 1980). Information on the damage which can be done to the health of sea animals is found in a number of other publications (Vsevolodov 1948; Chupakhina 1969; Zablotski 1971; Temirova and Usik 1971; Gurevich and Evdokimov 1972; Nikolski and Kandinski 1974; Popov 1975; Starostin 1975; Delamure et al. 1976; Kovalaeva et al. 1978; and others). The data which have been introduced unquestionably confirm that the helminths emerge as one of the primary factors in the mortality of marine mammals, a fact that must be taken into account when one is establishing or studying their numerical or population dynamics.

Having gathered and analyzed a large amount of material we naturally arrived at the necessity of forming generalizations about it from the viewpoints of ecology, zoogeography, and phylogeny (Delamure 1952, 1955, 1956; Delamure and Skriabin 1958; Skriabin 1958). The results established the rules [regularities] of the patterns of the helminth faunas of the pinnipeds and cetaceans and likewise the patterns of distribution of helminths in the animals of the World Ocean. This showed that among the species and genera of helminths there are some which are dispersed in bipolar, amphiboreal, and amphi-Pacific [fashion]. This was accomplished for the first time on the basis of helminthological material and it was also explained in light of the history of the free-living fauna of the World Ocean (Berg 1922, 1934; Andriashev 1939; Zenkovich 1947, 1951; and others).

Comparison between the helminthofauna and the large taxa of their hosts in light of their ecology and phylogeny is of great interest. Here it has been established that, though the helminthofauna of pinnipeds shows characteristics of independence, it was developed principally from ancestors derived from the helminthofauna of terrestrial animals. In contrast with that of pinnipeds, the helminthofauna of cetaceans possesses clearly expressed traits of independence; it includes such helminth families as Pholeteridae, Brauninidae, Crassicaudidae, Pseudaliidae, and Campulidae almost completely. Investigations of the composition of the helmithofauna clearly reflect fundamental differences in ecology and phylogeny of these unique animals (Delamure 1955).

Sharp differences were demonstrated also when comparing the helminthofauna of toothed and baleen whales. Because of the small number of species (11), narrow specialization and feeding only at the surface of the sea on the not very varied [on the relatively homogeneous] plankton organisms—sometimes on mollusks and sometimes on schooling fishes, and other peculiarities of baleen whales; they have developed in themselves a helminthofauna which has no marked originality. It is totally different with the toothed whales. The numerous species of these cetaceans (69 species), which have settled widely in the World Ocean—even in brackish and freshwaters, have won for themselves the most varied ecological niches and accustomed themselves to feeding at different depths on varied kinds of food. In the process of evolutionary development of the toothed whales, they had a much greater opportunity than the baleen whales to become specific hosts for numerous species and genera and even a few families of helminths. There are essential differences between the helminthofauna of toothed and baleen whales which result from the long process of ecological selection, and it is possible to use them to compare the phylogenetic differences between the suborders of whales and also to compare their relationships with other animals (Delamure 1970).

Comparing the helminths of dolphins and beaked whales with the helminths of the Viverridae family [civets] in the historical [evolutionary] aspects, allows us to conclude [postulate] that these groups of hosts are close in phylogenetic respects (Delamure 1960).

Helminthological workers have discovered many valuable and interesting answers in their investigations of native mammals, which have involved their comprehensive studies of the parasites and also the characteristics of pinnipeds and cetaceans indigenous to the waters of the U.S.S.R. and also [those from] beyond their borders (Kleinenberg 1956; Tomilin 1957; Kleinenberg et al. 1964; Berzin 1971; Yablokov et al. 1972; Fedoseev 1975; Geptner et al. 1976; and others). These publications utilize and also exemplify the scientific investigations of parasites of marine mammals. It is not possible to encompass the subject without their numerous works in this area.

We have presented the work of the last 10 decades by Soviet helminthologists before many All-Union scientific conferences as well as those of several republics and now before the Soviet-American conference, conducted within the framework of the agreement, in surroundings that provide immeasurable support and assistance.

From this accounting it is evident that studies of the helminths of pinnipeds and cetaceans are of notably practical importance. It is possible to report with confidence that study of the helminths of animals, especially those of industrial importance living in the waters of the Soviet Union, compare favorably with those of our friends, and that this is possible thanks to the support and assistance provided by the Laboratory of Helminthology of the U.S.S.R. Academy of Sciences, and the Ministry of Fisheries of the U.S.S.R., the Ichthyological Commission, VNIRO and the foundation related to it, the Zoological Institute of the U.S.S.R. Academy of Science, Vsyesoyunznogo Institute of Helminthology, the Limnological Institute CO [SO] Academy of Sciences of U.S.S.R., the Astrakhan Zapovyednika, Ministry of Enlightment [or Instruction] of the U.S.S.R., and the administration of the Simferopol University and the institutions of our associates.

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